MODE OF LIFE, FEEDING, DIGESTION AND SYMBIOSIS WITH ZOOXANTHELLAE IN THE TRIDACNIDAE

BY

C. M. YONGE, D.Sc.(Edin.)

Professor of Zoology in the University of Bristol ; late Balfour Student in the University of Cambridge.

WITH TEN TEXT-FIGURES AND FIVE PLATES.

CONTENTS.

1. INTRODUCTION.

THE members of the Tridacnidae are amongst the most important constituents of the fauna of coral reefs in Indo-Pacific regions. On the reefs of the Great Barrier no animal is so conspicuous as the giant clam, *Tridacna derasa*, and few more ubiquitous than the horse-hoof clam, *Hippopus hippopus*, or the common burrowing clam, *Tridacna crocea*. Yet surprisingly little is known about these animals. On account of their immense size

the shells of the larger species have been known for many centuries past and have always aroused the interest of conchologists,* but knowledge of the morphology of the Tridacnidae rests largely on a few papers, notably those of Quoy and Gaimard (1834), Woodward (1855), Macdonald (1857), Vaillant (1865), Grobben (1898) and Lacaze-Duthiers (1902). Hedley (1921) has revised the taxonomy of the Australian Tridacnidae and given some account of the habits of certain species. The universal presence of zooxanthellae in the Tridacnidae, almost certainly unique amongst Lamellibranchia, and responsible, as will be shown in this paper, for the remarkable peculiarities of structure possessed by this family, has been briefly described only by Brock (1888), although Boschma (1924) refers to it, while I have recently given a short general account of this association elsewhere (Yonge, 1932a).

The work with which this paper is concerned was carried out largely on three species, *Hippopus hippopus, Tridacna derasa* and *T. crocea,* especially the last-named. Owing to the limited time available, attention was confined to problems of especial interest, namely, the boring habits of *T. crocea,* the structure and function of the organs of feeding and digestion and, above all, the nature of the relationship between the zooxanthellae and the Tridacnidae.

2. MODE OF LIFE.

As Hedley has already stated, the Tridacnidae may be divided into two groups, the smaller species which burrow into coral rock and the larger ones which lie free on the surface of the reefs. According to him the former include *T. maxima, T. elongata* and *T. crocea,* and the latter *T. derasa, T. gigas, T. mutica* and *T. squamosa,* together with *Hippopus hippopus.* Mr. T. Iredale, who is preparing the systematic report on the Mollusca, does not agree with Hedley's nomenclature. According to him *T. maxima* should be called *T. fossor, T. elongata* is a non-burrowing species, while the true giant clam called *T. gigas* by Hedley should be named *T. derasa.* Iredale's names are used throughout in this paper, attention being confined to those species which could be identified with certainty, and the general distribution of which has been described elsewhere in these reports by Stephenson, Stephenson, Tandy and Spender (" The Structure and Ecology of Low Isles and Other Reefs ", Vol. III. No. 2).

(a) SURFACE FORMS.

The shells of species with this mode of life can readily be distinguished from shells of burrowing species by the much smaller size, or complete absence, of the pedal aperture. This is correlated with the absence of any byssus in the fully-grown animal, although there can be little doubt that all are attached by this means during early life. After they attain a certain size apparently their weight alone is sufficient to maintain them in position and the byssus must atrophy. Thus *Hippopus hippopus,* which is extremely common especially on sandy areas on the surface of reefs (Plate III, fig. 7), has no pedal opening (Plate IV, fig. 8) and is never attached. *Tridacna derasa* probably most frequently occurs wedged in between boulders, where it constitutes a grave danger to the unwary, having been responsible for a number of deaths along the Great Barrier and elsewhere,

* The Greeks, who conquered Persia under Alexander the Great, found " oysters " in the Indian Ocean more than a foot long. This is probably the earliest record of the occurrence of the Tridacnidae. A very interesting account of early observations on the Tridacnidae is given by Vaillant (1865).

but is most conspicuous when it occurs, not at all infrequently, on the flat surface of the leeward side of the outer reefs. This species is the largest lamellibranch of this or any other period in the world's history. Rumour has credited it with a maximum length of 14 ft., but the largest authentic specimen recorded had a length of $4\frac{1}{2}$ ft., was 2 ft. 5 in. broad and probably weighed about 4 cwt. The largest specimens personally examined were a little over 3 ft. in length (Plate I, fig. 1), and so heavy that the combined efforts of two men failed to raise them. Specimens of this size have no pedal aperture, but a specimen shown in Plate I, fig. 2, which was 14 in. long, possessed a relatively small pedal aperture, about 5 cm. long and 1·2 cm. wide. This animal did not, however, possess a byssus and could be picked up.

All of these clams live normally resting on the hinge side of the shell, with the edges of the shell valves pointing directly upwards. The pedal aperture (where this is present), as shown clearly in Plate IV, fig. 9, and Text-fig. 3, lies close to the umbo. In other words, as a result of a turning movement in the longitudinal plane, the dorso-ventral relations of the visceral mass and associated organs, on the one hand, and of the mantle and shell, on the other, have become, as examination of Text-fig. 3 will reveal, the exact opposite of those in the other lamellibranchs. This fact has given rise to considerable controversy. Blainville (1825), Vaillant and Grobben believed that the visceral mass had moved relative to the shell, and considered the umbo and hinge to be dorsal, as in the other lamellibranchs, and the edge of the shell valves ventral. In the opinion of Lacaze-Duthiers the mantle, and hence the shell, has moved relative to the visceral mass so that the umbo is ventral and the edge of the shell-valves dorsal. These workers knew nothing of the habits of the living animal, and could not advance any but purely morphological reasons for their conclusions. I have been more fortunate in this respect, and, as will be shown later in this paper, there is ample reason for considering that it is the *mantle* which has changed its position in relation to the rest of the body and not *vice versa*. I am thus in agreement with Lacaze-Duthiers in regarding the hinge and umbo as being ventral. To avoid confusion the terms " hinge side " and " free edge " of the shell will be used, the former being morphologically ventral and the latter dorsal.

Except when they live between tide-marks and for the period when they are exposed by the retreating tide (Plate I, fig. 1, Plate II, fig. 3), the shell valves of *all* the Tridacnidae are *invariably* open and the thickened mantle edges widely exposed to the light. This is particularly well shown in the photographs reproduced in Plate I, fig. 2, and Plate II, fig. 4, which were taken looking directly down upon clams expanded under water. The extent to which the peculiarly thick and fleshy mantle lobes are reflected over the edge of the shell-valves will be noted (this is also very well shown for *T. fossor* in Plate XVIII, figs. 3 and 4, of Paper No. 2 in Vol. III of these Reports). This is a universal characteristic of all species of *Tridacna*. In *Hippopus* this is not the case, but, as shown in Plate III, fig. 6, the shell valves separate more widely. In both cases the mantle-tissue is exposed to the greatest possible extent to the direct rays of the sun. There can be no doubt that the habits of these animals are directed especially to this end, and for reasons which will be dealt with later. The exposed mantle-lobes are invariably richly coloured. In *T. derasa* they are consistently of a brown to olive-green colour, with bright emerald-green spots and occasional lighter areas ; in *Hippopus* they are always olive green. The flesh is particularly tough and very difficult to cut.*

* Although so freely exposed I never saw any indication that these tissues were bitten by fish.

(b) BORING FORMS.

T. crocea is the commonest of the boring species and the one most highly adapted for that mode of life. *T. fossor*, which is also a common species, occurs usually embedded in coral fragments which have been partially cemented together, but *T. crocea*, as shown in Plate II, figs. 3 and 4, and Plate III, fig. 5, bores into solid coral boulders until the edges of the shell-valves lie flush with the surface of the rock. The abundance of this species is indicated by the photograph reproduced in Plate II, fig. 3, and also by the statement that in one piece of rock roughly rectangular in shape and measuring about 30 cm. by 45 cm., sixteen medium and full-sized specimens were counted. The animal commonly attains a length of 10 cm., a width of over 4 cm. and a depth of 7 cm., so that in the above case, which was by no means exceptional, they existed literally " cheek by jowl " in the rock. Specimens settle wherever there is even the smallest area of coral rock not covered with living coral tissue, and instances such as that illustrated in Plate III, fig. 5, where the clam lies in the dead centre of a living coral colony, are not at all uncommon.

The mantle-lobes can be expanded over the edge of the shell-valves in this species (and in *T. fossor*) to an even greater extent relatively than in *T. derasa*, as shown in Plate II, fig. 4, where the shell-valves are entirely obscured by them. In my experience the colour of the tissues was deep blue or bluish green, but Prof. Stephenson, who spent a great deal of time in the course of his ecological work observing the fauna of the reefs, assures me that, though most often blue, it may be black and also other colours, such as a pattern of pink and green frecklings and splashes. But it certainly does not exhibit the extraordinary variety of colour and pattern possessed by the somewhat larger and much more conspicuous *T. fossor*, where almost every colour and variety of colours, other, in my experience, than red, are to be found. (The wide range in pattern is well shown in Vol. III, No. 2, Plate XVIII, figs. 3 and 4.) All boring species, in all stages of growth, have a large pedal aperture. That of a fully grown *T. crocea* is shown in Plate IV, fig. 9, the shell in this case being 10 cm. long, and the pedal aperture 4·5 cm. in length and 1·6 cm. at its widest point. After removal from rock these animals are at the mercy of small crabs and other carnivores, which enter by the pedal aperture and eat out the tissues.

The boring habits of *T. crocea* were studied in some detail. Work had already been done on this subject by Hedley, but, as will be shown, my conclusions differ fundamentally from his. A careful search of rocks in the boulder zone was made for young specimens and, after a little practice, surprisingly large numbers were found, varying in length between 1 and 2 cm. These individuals had not begun to bore, but were living in holes on the surface of the boulders or in the beach limestone, notably in empty barnacle shells, as shown in Text-fig. 1, or in disused burrows of *Lithophaga* and other rock-boring animals. In all cases they were attached by a byssus, but easily detached. Observation of specimens in captivity revealed that at this stage they possess a wedge-shaped foot capable of considerable extrusion, an animal 1 cm. in length being able to extend its foot for 0·7 cm. Byssus threads were readily formed, and the animals were able by this means to clamber up the sides of a bowl in the same manner as young *Mytilus*. They usually clambered right out of the water, then secured themselves with a byssus and fell back just below the level of the water and there remained. This may well be the normal

procedure in nature, for *T. crocea* is especially common between tide marks, and often high up on the large rocks in the boulder zone.

The size at which burrowing begins seems to vary. The largest surface-living specimens taken were about 2 cm. long, whereas the smallest animal found within the rock, which had already excavated a burrow almost as deep as itself, was only 1·4 cm. long. A comparison between this animal and surface-living specimens revealed that, correlated with the assumption of the burrowing habit, are a greater folding over of the sides of the pedal opening on the hinge side of the shell by the mantle-lobes, a considerable reduction in the size of the foot, a great increase in the size of the byssus and a wider gape of the shell-valves. The reduction in the relative size of the foot is progressive, for it may still be protruded for some distance by a young animal after removal from the burrow, but this was never observed in fully-grown animals.
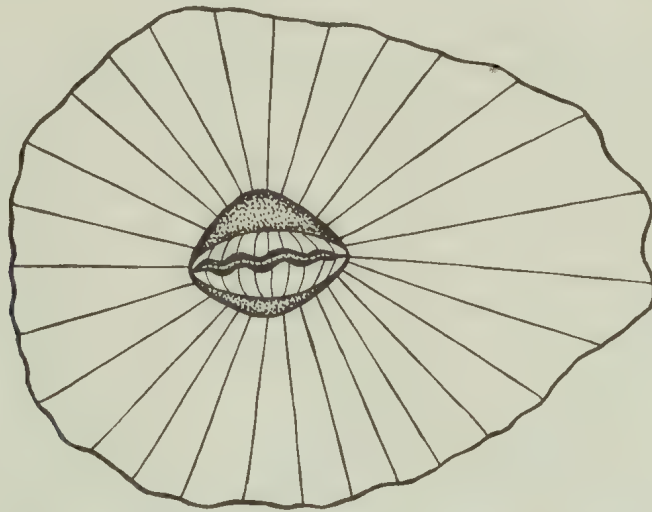

TEXT-FIG. 1.—*Tridacna crocea*, very young specimen (0·9 cm. long) which has not begun to burrow, but has settled, attached by the byssus, in the cavity of an empty barnacle shell. × 3.

The nature of the burrow excavated in the rock can best be understood by reference to Text-fig. 2. The asymmetry of the shell is reflected in the shape of the burrow, the free edges of the shell-valves lying just flush with the surface (Plate II, fig. 3). The burrows are always perfectly smooth within, and large enough for the shell-valves to be fully extended and appreciable backward and forward movements to be executed. The opening (Text-fig. 2, o–o) is considerably shorter and narrower than the full internal dimensions of the burrow, or indeed of the animal which can only be extracted by breaking open the burrow. An adult animal is invariably imprisoned within its burrow. The most notable feature of the burrow is the projection (R.) which occurs immediately posterior to the position (U) where the umbo of the shell is situated. It is to this projection that the massive byssus (Text-fig. 3, B) is always attached.

Hedley, after rightly condemning Vaillant's statement that *Tridacna* cannot bore, but becomes gradually enclosed in rock by the upward growth of coral around it, proceeds to attribute the capacity for boring in *T. crocea* to the abrasive action of what he describes as " the mushroom-shaped foot ". He does not state exactly how this takes place, but illustrates this foot (Hedley, 1921, pl. xxxi, fig. 9) by a photograph of a model of a burrow " cut open to show the natural position of the shell and animal ". This model was on exhibition at the Australian Museum, Sydney, in 1929. During the course of my work

I examined many hundreds of *T. crocea*, and never saw anything in this, or any other species of *Tridacna*, remotely resembling this mushroom-shaped foot. The foot in the adult *T. crocea*, as shown in Text-fig. 3 (F), is pointed and relatively much smaller than in the young, its sole function in the adult, so far as can be ascertained, being the development within it of the greatly enlarged byssus gland, which secretes the massive byssus shown in Text-fig. 3 (B). The byssus is invariably highly developed in all burrowing species. It was always necessary after opening the burrows to cut the byssus or break it off by twisting the shell with considerable force. It is very difficult to imagine how so distinguished a conchologist as Hedley could have failed to see or omitted to describe this byssus, and could have given so completely erroneous a description of the foot.

The burrows are excavated mechanically. Chemical activity, which the calcareous nature of the rock would permit, is improbable in the first place because the shell is not
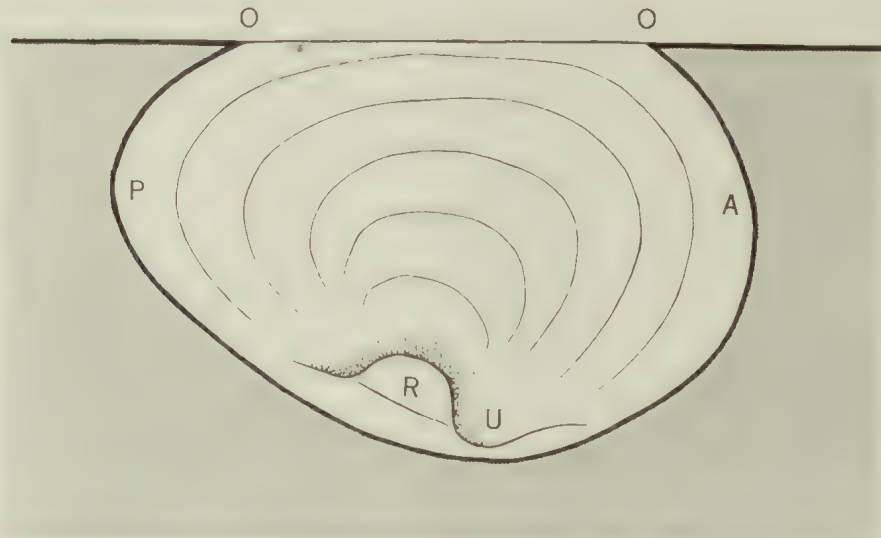
Text-fig. 2. Diagram showing the nature of the burrow excavated by *Tridacna crocea*; rock represented by stippling. × ⅔. A, anterior end of burrow; o o, extent of opening; P, posterior end; R, pillar of rock to which byssus attached; U, cavity in which the umbo is situated.

covered with the horny periostracum typical of the lamellibranchs which bore by acid secretion, such as *Lithophaga*, while the testing with Gunzberg's reagent of the foot and the mantle edges round the pedal opening, the only tissues which are in direct contact with the interior of the burrow, failed to reveal any indication of free acid.

Boring almost certainly proceeds in the following manner : A young animal attaches itself in a suitable hollow in the rock by means of a stout bundle of byssus threads. With the aid of this strong purchase the animal then proceeds to grind its way downward into the rock by rocking to and fro both laterally and longitudinally. The shells of *T. crocea* are always ridged, owing to the mantle edges, which secrete the shell, curling back over the edge of the valves. In a fully-grown specimen these ridges, as shown in Plate IV, fig. 10, are ground smooth over the lower two-thirds of the valves, whereas round the free edges, which take little or no part in the abrasive action, the ridges may be 4 mm. or more in height though only about 1 mm. thick.* The coral rock, even that formed

* In *T. elongata*, which does not bore, there are prominent ridges almost to the umbo.

by *Porites*—which is the densest—is comparatively friable, while the shells of *Tridacna* are exceptionally dense—much more so than the shells of *Gastrochoena* or *Pholas*, which also bore mechanically and often into much denser kinds of rock. Moreover, the byssus in *T. crocea* is much thicker than is necessary merely for attachment. In the common black-lip pearl oyster, *Pinctada margaritifera*, where attachment is the sole function of the byssus, this is never more than about one-third the size of that of *T. crocea*, although the two animals are about the same size.

One difficulty remains. If the animal is always attached about the mid-ventral line by the byssus on which it works, how does it penetrate to any depth without under-cutting the byssus and so losing its attachment ? That the region where the byssus is attached is not cut away is revealed by the invariable presence in the burrows of the pillar of rock (Text-fig. 2, R) to which this is attached. The explanation of this difficulty may be furnished by one of two factors, or by a combination of the two. These factors are the differential growth of the shell, and the oblique entrance, already noted by Hedley, of *T. crocea* into rock. Evidence for the former was obtained by measurements, the distance between the anterior end of the shell, to the beginning of the pedal gape being 37·5%, 42·5% and 45% of the total length of the shell in animals 1·6 cm., 4·0 cm. and 10 cm. in length respectively.* The difficulty of the byssus attachment can be overcome on the basis of either of these factors. The byssus gland will be pushed further and further towards the posterior end as growth and burrowing proceed. Consequently, though the original anterior side of the byssus attachment will continually be undercut by the umbonal region of the shell (as indicated in Text-fig. 2), and the byssus threads there attached will lose their connection and probably be detached by the animal new threads will be added to the byssus on the posterior side. In this way the animal will be enabled to sink deeper and deeper into the rock without losing the essential point of attachment. It is note-worthy that the pillar to which the byssus is attached is relatively much higher in the burrow of a fully-grown than in that of a young animal, indicating that either differential growth slows down or the angle of entry into the rock becomes more vertical, the position of the byssus in either case no longer altering so rapidly, and the animal tending to settle down as deeply as possible around the byssus. As a result of this it cuts out in the form of a tall pillar the area of rock to which the byssus threads are attached.

The immense size of the retractor muscles of the foot (Text-fig. 3, RM) lends support to this explanation of the mechanism of boring. The two muscles are inserted into the shell valves, on each side, immediately anterior to the insertion of the single adductor (AD) which is characteristic of the Tridacnidae. Indeed they appear at first sight, as will readily be realized by reference to Text-fig. 3, like a portion of the adductor, the general appearance of the two muscles resembling that of the single adductor in lamellibranchs, such as *Pecten. Spondylus* or *Ostrea*, with its division into " quick " and " catch " muscles. Actually the retractor muscles of each side bend round ventrally and are attached side by side into the foot. These exceptionally powerful pedal retractors will provide the force necessary to draw the shell tightly against the rock and so enable the shell-valves to grind out the burrow. The unevenness of the under-surface will cause a longitudinal rocking, while a lateral rocking, which probably takes place, can be brought about by alternate contractions of the pedal muscles of the two sides. It is noteworthy that the

* Unlike the surface species, where it becomes smaller, the pedal gape in *T. crocea* increases both absolutely and relatively as growth proceeds. This is shown in Hedley's figures (pl. xxxiv).

retractor muscles of the foot in *Hippopus*, which does not burrow, are not more than one-quarter the size of those of *T. crocea*; the figures of Lacaze-Duthiers exaggerate their size.

This mode of boring is unique amongst lamellibranchs. In all other rock- (and also wood-) boring bivalves, no matter whether they bore by chemical agencies, like *Litho-phaga*, or by mechanical agencies like *Pholas*, *Gastrochoena*, *Martesia* or *Petricola*, the anterior end is responsible for burrowing, while the siphons project from the posterior end and enable the animal to draw in the necessary water currents. In *Teredo*, the most specialized of all borers, the animal is actually greatly elongated in an antero-posterior direction. Only in the Tridacnidae is the hinge side responsible for boring, and this, as will be shown later, is clearly the result of the twisting round of the mantle, a process which must have taken place *before* the development of the boring habit.

3. FEEDING.

Work on feeding was confined to *T. crocea*, comparative data being obtained from other species. The morphology of the organs of feeding calls for little comment, having already been adequately dealt with by Vaillant and Lacaze-Duthiers. The positions of the inhalent and exhalent apertures are interesting. The mantle-lobes are fused for the greater part, but, in addition to the wide pedal aperture on the hinge side, there is an exhalent aperture (Text-fig. 3. EA) a little to the anterior of the mid-dorsal line (I follow Pelseneer in regarding the position of the mouth as indicating the anterior end in Lamellibranchia), and an inhalent aperture (IA) near the posterior end on the dorsal surface. The former, as shown clearly in Plate I. fig. 2. and in Plate II. fig. 4. is circular in cross-section and situated on the end of a conical siphonal process (Text-fig. 3. SP). The inhalent aperture is a longitudinal slit. It is shown closed in Plate I. fig. 2 (*T. derasa*), and open in Plate II. fig. 4 (*T. crocea*). From time to time water is ejected with great force through these apertures as a result of sudden contractions of the adductor muscle.* This is most obvious in the case of the larger species, the presence of which could always be detected on the reef surface when the animals were just covered with the rising or retreating tide by the periodic spouts of water which rose high above the surface.

The gills of the Tridacnidae are not S-shaped in longitudinal outline, as stated and figured by Lacaze-Duthiers, this appearance, as he actually suspected, being due to contraction in preserved specimens. The appearance of the gills in life in *T. crocea* (and there is no material difference in their disposition in other species) is shown in Text-fig. 3. The gills of the Tridacnidae are interesting, because, as previously noted by Woodward in *T. crocea* and by Lacaze-Duthiers in *T. elongata* and *Hippopus*, the outer demibranchs (OD) are incomplete. They consist of a single lamella (probably the descending one). The inner demibranchs (ID) are normal in structure, the ascending and descending lamellae uniting in a deep, well-defined food-groove (FG). The reduction in the outer demibranch is greater in *T. crocea* than in the other species examined. The gills possess, therefore, essentially the same structure as those of *Lyonsia*, *Pandora* and *Scrobicularia* (Ridewood, 1903). The gills are very fleshy, the individual filaments being exceptionally broad; their structure has already been described by Ridewood for *T. elongata* and calls for no further comment.

* Vaillant and more recently Tamura (1931) have studied the power of this muscle, the latter in several species of *Tridacna*.

In *T. derasa*, on the other hand, the outer demibranch is similar in all respects to the inner, both being fully developed with a deep food-groove at the free margin and of immense size. I preserved a portion of the gills of a specimen opened on one of the Outer Barrier Reefs. The shell of this animal was 3 ft. long, the gills (after preservation in alcohol) having a maximum height of 4·3 cm. and a maximum breadth of 1·2 cm. The individual
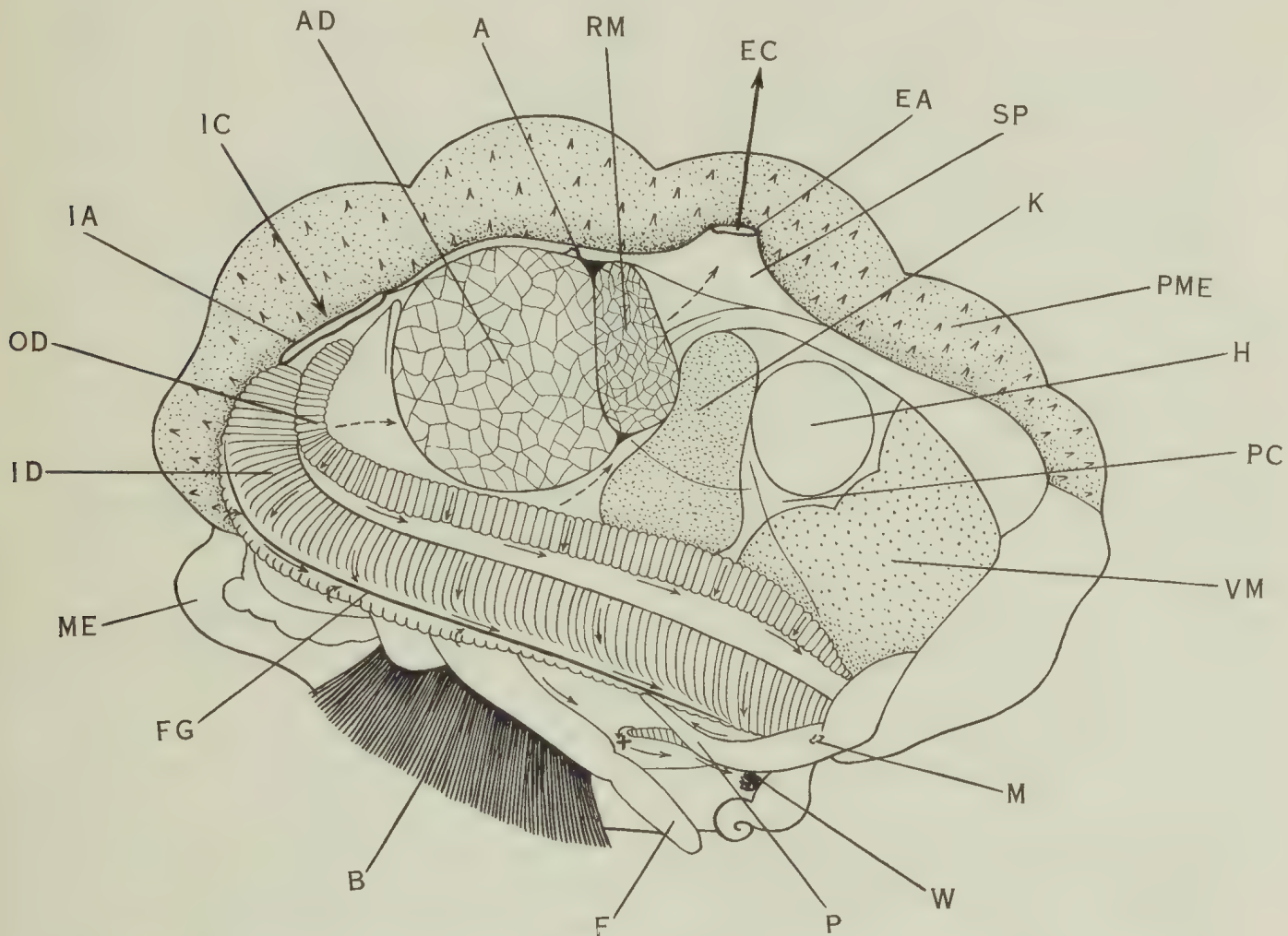
TEXT-FIG. 3.—*Tridacna crocea*, drawing, from life, of an individual lying on the left shell valve, right mantle lobe removed. × 2. A, anus; AD, adductor muscle; B, byssus; EA, exhalent aperture; EC, exhalent current (represented by arrow); F, foot; FG, food-groove on inner demibranch; H, heart; IA, inhalent aperture; IC, inhalent current (represented by arrow); ID, inner demibranch of gill; K, kidney; M, position of mouth; ME, mantle edge, unpigmented, bordering the pedal gape on the underside; OD, outer demi-branch; P, labial palps; PC, pericardium; PME, pigmented mantle edge of upper, exposed side; RM, retractor muscle of foot; SP, siphonal process of exhalent aperture; VM, visceral mass; W, accumulation of waste matter rejected by palps. Small, complete arrows show direction of food-collecting currents on the gills, broken arrows currents in the exhalent chamber.

filaments were about 4 mm. broad. This difference between the gill in *T. derasa* and in the other Tridacnidae has not previously been recorded, and it was unfortunately discovered too late for an examination to be made of the conditions in all species. I know of no other genus of lamellibranchs in which there is so great a difference between the form of the gill in different species. There seems no reason, however, for "splitting" the genus on

this character. The gills of the lamellibranchs are organs of feeding and, as such, more liable to modification than almost any other organ in the body. A possible explanation of the difference in form of the gill in the various species of the Tridacnidae will be given later.

The palps (P) in all the Tridacnidae have the same shape; they are free and very long. Those of *T. crocea*, which alone were studied in life, are very active, and readily curl back when much material is placed upon them. The general direction of ciliary currents on the gills and elsewhere is indicated by the arrows in Text-fig. 3. Water enters by the inhalent aperture (IA), and is drawn through the gills in the usual way into the exhalent chamber, whence, as shown by the broken arrows, it proceeds to the exhalent aperture (EA). Particles retained on the surface of the gills are carried into the food-groove (FG) on the inner demibranch (ID), but are passed to the gill axis from the surface of the incomplete outer demibranch (OD). In both cases they are carried forwards in the usual manner, being finally deposited between the pair of palps on each side. These are ridged on the inner surface, and only the minutest particles escape the selective activity of the cilia in this region and reach the mouth (M). The very small size of this has been commented on by both Vaillant and Lacaze-Duthiers; it lies at the point of the union of the two pairs of palps and is entirely obscured by these organs.

In *T. crocea* particles are transfered to the mantle surface first by the gills, if they are very large (relatively), and then by the palps, the tips of which curl back for this purpose, as shown at x in Text-fig. 3. Waste matter is then carried by ciliary currents to the extreme anterior end of the pedal gape, where it accumulates into masses (W). This system of rejection tracts is essentially similar to that of other lamellibranchs (see Yonge, 1928*a*, for a review of this subject), the only point of special interest being the accumulation of matter at the anterior end of the inhalent chamber instead of at the posterior end (siphonate Lamellibranchs), or about the middle of the ventral surface (*Ostrea* and similar genera). In all lamellibranchs accumulations of waste matter are removed from time to time from the inhalent chamber by sudden closures of the shell-valves, and in the Tridacnidae these are responsible for the sudden spoutings of water already referred to. The presence of the large pedal gape in *T. crocea* will enable this animal to remove waste matter from the inhalent chamber through this opening, water expelled by the sudden contractions of the adductor muscle making its way upward between the shell and the sides of the burrow and carrying waste matter with it. In animals which have no pedal gape, such as *Hippopus*, it is clear that waste matter must be carried, as in the majority of other lamellibranchs, to the posterior end of the inhalent cavity, and expelled from time to time by way of the inhalent opening. Unfortunately pressure of work prevented me from determining this point experimentally.

4. ALIMENTARY CANAL.

A straight oesophagus (Text-fig. 4, O) opens into the capacious stomach, which extends, in an antero-posterior direction, through the length of the visceral mass. The appearance of this organ when opened up along the mid-dorsal line is shown in Text-fig. 4. The stomach of the lamellibranchs is not only the region where the enzyme from the crystalline style is liberated and mixed with the food, but also usually a sorting organ, continuing in this capacity the work begun by the gills and the palps. Nelson (1918)

first described, in *Modiola*, the presence of a complicated food-sorting caecum in the stomach of a lamellibranch; others have been described in *Mya* (Yonge, 1923), *Ostrea* (Yonge, 1926b) and *Ensis* (Graham, 1931), while in the carnivorous Septibranchia, which feed on large masses of food, this structure has been shown to be absent (Yonge, 1928b). A careful study of the ciliary currents in the stomach of *T. crocea* was made,
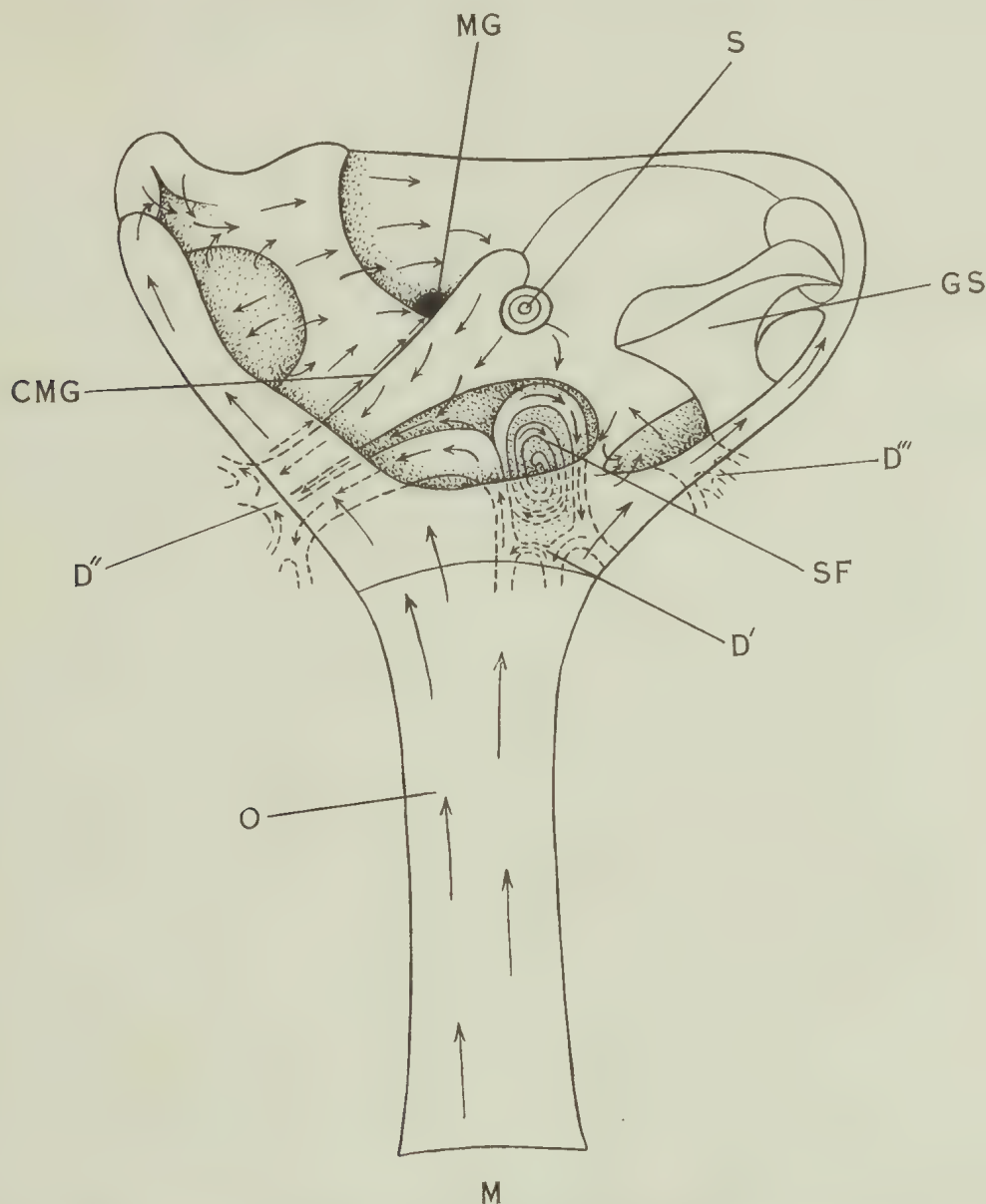
TEXT-FIG. 4.—*Tridacna crocea*; stomach opened along the mid-dorsal aspect. × 5. CMG, ciliary current leading into mid-gut; D', D'', D''', ducts leading into digestive diverticula; GS, gastric shield; M, mouth; MG, opening of mid-gut into stomach; O, œsophagus; S, style projecting from style-sac; SF, spiral fold. Arrows indicate direction of ciliary currents.

and the direction of these is indicated by the arrows in Text-fig. 4. The first point of interest that emerges is the complete absence of the food-sorting caecum which occurs in all other lamellibranchs which have been examined for it, with the exception of the highly specialized Septibranchia. What may possibly be a vestige of it is represented by a spiral fold (SF) present on the mid-ventral surface. Particles which are caught in the ciliary currents upon this are all, however, carried into the first of the series of ducts (D') which lead into the digestive diverticula. There are three of these series of ducts

(D', D", D'''), and all are exceptionally wide. This is indicated not only by their appearance, but by the fact that large masses, for instance the carborundum powder used to demonstrate the direction of the currents, pass readily into them. Material of this size *never* enters the ducts in animals such as *Mya* and *Ostrea*. The ducts are actually even wider in the Septibranchs, but there conditions are totally different. Moreover, material which is passed out of the first series of ducts passes along a groove and makes its way into the second series (D"), and only after rejection there is it caught (as in other lamellibranchs) in the ciliary current (CMG), which runs along the side of the ridge which leads to the opening of the mid-gut (MG). The third series of ducts (D''') is independent of the first two, and occurs (as in other lamellibranchs) at the base of the gastric shield (GS). Here, again, there are powerful ingoing currents round the anterior margin, material, as in the other ducts, being ejected at the opposite side. The structure of the stomach of *T. derasa* agrees in all respects with that of *T. crocea*. It is always a little difficult to determine from the study of the opened stomach exactly what takes place under normal conditions when it is an enclosed cavity, with the head of the style (s) projecting across it and bearing against the gastric shield. The general impression gained was, however, that, so far from there being any further sorting in the stomach, the ducts leading into the digestive diverticula are exceptionally wide, and every opportunity is taken of passing material into them. Only in the last resort is it passed into the mid-gut, where it passes beyond the possibility of digestive action. These conditions, so unlike those present in other ciliary feeding lamellibranchs, clearly show that the sorting mechanism on the gills, and especially on the palps, must be of the greatest efficiency. It is of the utmost importance that nothing but the most finely divided particles should enter the digestive diverticula, and the absence of any device to prevent this shows that the material which enters must be extremely fine. This fact was abundantly confirmed by the discovery, described in the next section of this paper, that even such small objects as blood-corpuscles of fish (readily taken into the stomach by other lamellibranchs, such as *Ostrea*), fail to pass the palps and enter the alimentary canal.

The nature of the stomach and the extreme efficiency of the sorting mechanisms in the mantle cavity are surprising (though a probable explanation will be advanced later). It would be expected that animals so large and so abundant as the Tridacnidae, living in water comparatively poor in phytoplankton and yet at a temperature which will involve a very high rate of metabolism, would have tended to acquire feeding and digestive mechanisms capable of utilizing larger particles of edible matter than other ciliary feeding lamellibranchs. The actual conditions indicate degeneration rather than increased efficiency.

The digestive diverticula, the ducts of which have already been described, form a dark brown mass which surrounds the stomach. Sections reveal that the tubules have the usual histological structure (see Yonge, 1926a). The interesting fact is that they are *greatly reduced in numbers*, the greater part of the region around the stomach being occupied by immense quantities of blood-cells. This matter will receive attention later.

The remainder of the alimentary canal does not call for any particular comment. The style-sac is attached for some distance to the mid-gut, later passing downwards into the substance of the foot, where it terminates. The style in the Tridacnidae is exceptionally large and firm. As recorded elsewhere (Yonge, 1932b), one taken from a specimen of *T. derasa*, 3 ft. in length, was 34 cm. long, had a maximum breadth of 0·5 cm., and

weighed, after dehydration in alcohol, 2·94 grm. The mid-gut, after traversing the visceral mass in various directions, merges into the rectum, which passes through the ventricle. The anus is situated about the middle of the dorsal side of the adductor muscle, a little posterior to the exhalent aperture. In other lamellibranchs the anus is situated normally at the posterior end of the adductor, and its change in position in the Tridacnidae is clearly associated with the shifting from a posterior to a dorsal position of the exhalent siphon. The fact that the exhalent siphon is now actually anterior to the anus indicates that it has made a greater relative change in position than has the anus.

5. ASSIMILATION.

Feeding experiments were carried out, using the blood-corpuscles of sting rays, and also iron saccharate, suspensions being made in jars of sea-water in which animals were kept. Small specimens of *T. crocea* (about 1 cm. in length) were used, and also fully-grown individuals, the former being later fixed entire and only portions of the stomach and digestive diverticula in the latter. As in all ciliary feeding lamellibranchs, the suspended material was rapidly collected in the mantle-cavity. The iron saccharate passed into the alimentary canal, where, as in all lamellibranchs previously examined (Yonge, 1926*a*, 1926*b*, 1928*b*), it was later found within the cells of the digestive diverticula and nowhere else. The absence of any sorting mechanism in the stomach and the great size of the ducts leading into the digestive diverticula had led me to the opinion that the Tridacnidae (owing, it at first appeared, to their great size) took larger particles into the diverticula than any other lamellibranchs, with the exception of the Septibranchia. Sections of the small specimens revealed, however, that although great numbers of blood-corpuscles were present in the gills, notably in the food grooves, none were to be found in the gut. Sections of portions of the stomach and digestive diverticula from large animals showed a similar absence of ingested corpuscles. In lamellibranchs such as *Mya* (Yonge, 1926*a*) and *Ostrea* (Yonge, 1926*b*) blood-corpuscles of Elasmobranchs are taken freely into the stomach, and there ingested by phagocytes, which then pass back with them through the walls of the stomach. They also penetrate the ducts of the digestive diverticula, where again they are ingested by wandering phagocytes, but they never enter the actual diverticula. In the Septibranchia (Yonge, 1928*b*), and also in some extent in *Teredo* (Yonge, 1926*a*), the lumen of the tubules is wider, and corpuscles enter and are ingested and then digested intracellularly by the cells which line them. It was expected that, in the Tridacnidae, corpuscles would certainly be taken into the stomach and there ingested by phagocytes (which, as shown below, occur in large numbers), and that, owing to the wideness of the ducts, they would probably penetrate into the diverticula. The negative results obtained indicate the probability of some additional means of nutrition. The nature of this will be abundantly demonstrated in the sections of this paper devoted to the zooxanthellae.

Examinations of the gut contents were made in all three species. In *T. crocea* the stomach contents consisted almost exclusively of vast numbers of phagocytes with a few living flagellates and ciliates (the latter probably commensals). Finally there were a number of brown spherical algae corresponding in all respects to the zooxanthellae present in the tissues. Many of the phagocytes contained these, or possibly other vegetable matter, in various stages of digestion. One of these is shown in Text-fig. 5. Apart from

these algae nothing of any significant food value was found in the stomach of the animals examined. In a solitary specimen of *T. derasa* which was opened for examination the stomach contained many of these zooxanthellae, the majority intact, but a few ingested within phagocytes. A few diatoms were also found and some fine filamentous threads of algae. In *Hippopus* many intact zooxanthellae were found in the stomach, some of them actually dividing : there were few phagocytes free in the lumen in any of the
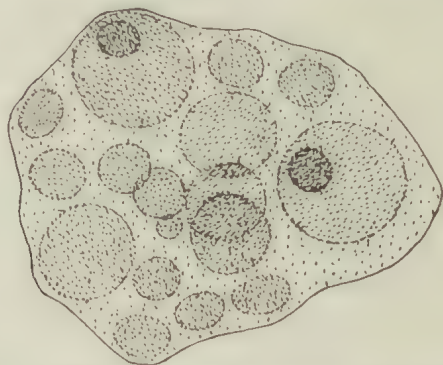
TEXT-FIG. 5.   *Tridacna crocea* ; phagocyte from stomach, containing zooxanthellae in various stages of digestion.   Drawn from life.   × 2000.

specimens examined, and in none of these were algae ingested. Some intact zooxanthellae were actually present in the faeces. Boschma (1924) states that he found large numbers of zooxanthellae in all stages of digestion in the stomach of *Tridacna*. The digestive diverticula were also examined, both fresh and after maceration in Bela Haller's fluid, in both *T. crocea* and *Hippopus*. Zooxanthellae in all stages of digestion were present in the cells of adults in both species—a fact later confirmed by sections. It would appear, therefore, that little food enters the gut except zooxanthellae (the source of which will be discussed later), and that these may be ingested by the free phagocytes in the gut or by the cells of the digestive diverticula.

6. ZOOXANTHELLAE.

If the surface of the pigmented, exposed mantle-edges of any of the Tridacnidae is lightly scraped with a knife, a brown, mucus-laden mass accumulates on the blade. Examination under the microscope reveals that the brown colour is due to innumerable spherical zooxanthellae, apparently similar to those present in the corals and other coelenterates. The presence of these algae in the mantle-tissues was first reported by Brock (1888). His material was preserved in spirit, and he regarded them as green cells or " pseudochlorophyllkörper ". He noted that they were spherical, 6 to 9μ in diameter, with a well-defined nucleus and a chloroplast, and that they divided by transverse fission, He observed that they were confined to the blood-sinuses, and stated, erroneously as will be shown, that they never occurred intracellularly. So far as I am aware, Boschma (1924), who makes but a passing reference to the matter, is the only other worker who has mentioned the occurrence of this association.

This is the more remarkable because association between molluscs and unicellular algae is rare. Amongst gastropods algae occur in the tissues of a variety of opistho-branchs. They have been described in *Elysia viridis* by de Negri (1876) and Brandt

(1883), in *Aeolis glauca* by Hecht (1895), in *Melibe rangii* by Hornell (1909), in *Phyllirhoë* by Zirpolo (1923) and Fedele (1926), and in *Spurilla neapolitana* and *Favorinus albus* by Henneguy (1925). Naville (1926) has described the very interesting case of the Nudibranch, *Aeolidiella alderi*, which feeds exclusively on the Actinian, *Heliactis bellis*, and contains zooxanthellae derived from the tissues of the anemone in the cells of the digestive gland. During a recent visit to the Tortugas I obtained specimens of a nudibranch, the species of which I have as yet been unable to determine, which invariably contains zooxanthellae.

The presence of algae in these opisthobranchs, all of which are probably carnivorous, is, as I have pointed out elsewhere (Yonge, 1934), easier to explain than is their presence in lamellibranchs which are primarily herbivorous. The Tridacnidae are the only group known to contain zooxanthellae (careful examinations of the very numerous lamellibranchs at Low Isles failed to reveal any others), but Goetsch and Scheuring (1926), following up the older observations of Clessin (1873), have described the occasional presence of *Chlorella vulgaris* in the tissues of the freshwater lamellibranchs, *Anodonta cygnea* and *Unio pictorum*. Algal infection occurs in the posterior end of the mantle, especially near the siphons, in the hinder parts of the gills even, in a few cases, as far forward as the foot. It is confined to the regions where light can penetrate. The algae always occur *between* the cells, usually of the connective tissue, but occasionally of the epithelia of the mantle or the hind-gut, and frequently in groups or " nests " together. The infected tissue is often slightly oedematous. Goetsch and Scheuring came to the conclusion that the infection was of a parasitic nature, permitted in the first place by some enfeeblement of the animals, but that an association of a symbiotic nature might become established. In their opinion *Chlorella vulgaris* has a high resistance to the action of animal tissues and a strongly aggressive action upon them. Very similar conditions are occasionally found in the freshwater gastropod, *Limnaea peregra*, Boycott (1926) having described cases in which green spots appear on the foot, mantle edges, tentacles and other tissues which are exposed outside the shell when the snail crawls. Each of these consists of a small cyst embedded in the tissues and filled with a species of *Chlorella*. Here again there was clear evidence of parasitic infection and of a definite reaction by the tissues of the mollusc. Conditions in the Tridacnidae are far removed from those which occur in infected specimens of *Anodonta* or *Unio* ; algae are invariably present and. as will be shown, the association is of the most intimate character.

(a) STRUCTURE.

Despite their superficial resemblance, the zooxanthellae present in the Tridacnidae differ in a variety of ways from those which occur in the corals and other Anthozoa. A description of the latter is given in Paper No. 6 in this volume. The zooxanthellae (Plate V, fig. 11) are deep brown in colour and spherical with an average diameter of some 7μ. Tests for the presence of a cellulose wall were made with chlorzinc iodide, iodine with sulphuric acid, calcium chloride iodine, cuprammonia, and with iodine alone, but the results were negative in all cases. Brock reports similar negative results with chlorzinc iodide. This absence, or possibly very slight development, of a cellulose wall is confirmed by the somewhat irregular shape frequently assumed by the zooxanthellae in sections of preserved material. The zooxanthellae from corals, which have a

well-developed cellulose wall, are invariably regular in outline in sections. The nucleus, granular in character, is much larger than that of the zooxanthellae from corals, having a diameter about one-third that of the complete cell. The assimilation product and also the pyrenoid which it surrounds are to a corresponding degree smaller than those of the other zooxanthellae. The smaller size of the assimilation product was detected in fresh material. It is seldom preserved in fixed material, even after treatment with Fleming which almost invariably preserves it in the zooxanthellae from the corals, but sections reveal the smaller size of the pyrenoid.* The smaller size of these structures may possibly be correlated with the presence of relatively large accumulations of starch. This is revealed at once after treatment with iodine, very conspicuous blue patches appearing, notably around the pyrenoid. In zooxanthellae from corals no indication of starch was ever obtained, although the assimilation product, as previously reported by Boschma (1924), gave a somewhat indistinct reddish-violet colour with iodine, indicating the presence of some allied amyloid substance. Both types of zooxanthellae agree in the presence of many oil-droplets, revealed by blackening after osmic fixation and by a red colour after staining with Sudan III. In both also the cytoplasm is vacuolated.

There is no detectable difference between the life-histories of the two forms of zoo-xanthellae. Those from the Tridacnidae are frequently found dividing, notably in the superficial regions of the exposed mantle edges. Division is by simple fission, two oval-shaped individuals being formed, which then round off. The pyrenoid apparently divides before the nucleus, in which division is probably mitotic. No indication of spores, or of any sexual stage, has been found.

(b) DISTRIBUTION.

The zooxanthellae, as would be expected, are most numerous in those regions of the tissues most exposed to the light. These regions are actually greatly increased in the Tridacnidae by the remarkable enlargement of the mantle-edges, particularly on the free side. The mantle-edge in *Tridacna* is divided into three longitudinal folds (as in many other lamellibranchs, including the allied genus *Cardium*; Johnstone, 1899). The outer-most of these (Text-fig. 6, OF) is thin and secretes the shell; the middle one (MF) is thin on the dorsal side, but much thicker on the ventral side, where it extends beyond the edge of the shell in life, which explains the great development of retractor muscles within it. The inner fold is enormously developed dorsally (Text-fig. 6, IF) being the only portion of that region of the mantle shown in Text-fig. 3. It is so thick that it prevents the complete closure of the shell valves, as shown in Plate I, fig. 1, and Plate II, fig. 3. Internally it consists almost exclusively of blood-sinuses (the agents of extension) and of muscles (the agents of retraction), and is that part of the mantle which extends over the free edges of the shell in life, and so forms a broad, upwardly-directed sheet of highly pigmented tissue (Plate I, fig. 2, Plate II, fig. 4). This region of the mantle-edge is fused except at the inhalent and exhalent openings (Text-fig. 3, IA, EA). On the ventral side, around the wide pedal opening, this inner fold is not so well developed; it contains little muscle and no zooxanthellae.

* According to Haffner (1925), the *Chlorella* in *Chlorohydra* have smaller pyrenoids than the free-living individuals. This is associated with saprophytism. This is unlikely in *Tridacna*, where the algae always have abundant light and food salts.

In *Hippopus* the inner region of the mantle-edge on the free side is well developed, but, as shown in Plate III, fig. 6, it never extends beyond the edge of the shell valves, which are, however, capable of opening to a wider extent than in *Tridacna*, so that a
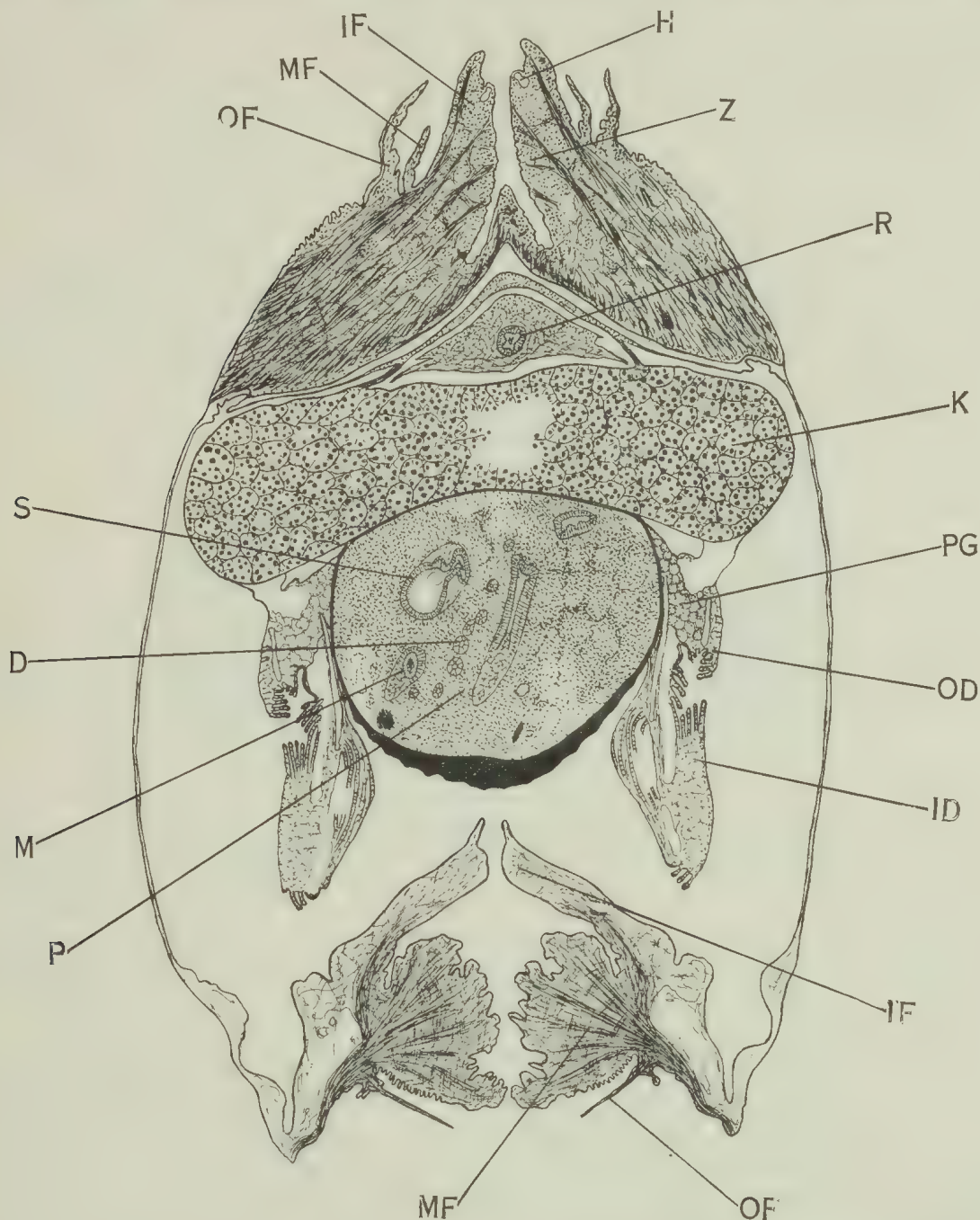

TEXT-FIG. 6.—*Tridacna crocea*; transverse section through young individual, 8 mm. long after decalcification, towards posterior end of the visceral mass. Fixed Bouin, stained Delafield's haematoxylin and eosin. × 20. D, digestive diverticula ; H, hyaline organ ; ID, inner demibranch of gill ; IF, inner fold of mantle edge ; K, kidney ; M, mid-gut ; MF, middle fold of mantle-edge ; OD, outer demibranch ; OF, outer fold of mantle-edge ; P, phagocytes ; PG, pericardial gland ; R, rectum ; S, style-sac ; Z, zooxanthellae in inner fold of mantle-edge on free (dorsal) surface.

considerable expanse of this tissue is exposed to the light. The mantle-edges can be entirely withdrawn and the shell valves close tightly.

There can be no doubt that this remarkable increase in the mantle-edge on the

exposed side of *Tridacna* is correlated with the presence within it of immense numbers
of zooxanthellae (Text-fig. 6, z). The blood-sinuses are literally packed with these algae
(Plate V, figs. 11 and 14) a fact originally noted by Brock, who speaks of the zooxanthellae
as serving the purpose of an injection to reveal the course of the blood-system. The
great extent of these tissues permits of the presence of correspondingly great numbers of
zooxanthellae, while the position of these on the upper side of the animal and their wide
and invariable exposure to the light when covered with water, particularly in *Tridacna*,
which is more highly adapted in this respect than *Hippopus*, provide ideal conditions for
photosynthesis. The Tridacnidae may be said to " farm " the algae within this greatly
enlarged inner fold of the mantle-edges.

Zooxanthellae also occur, though in smaller numbers, beneath the epithelium which
covers the dorsal portions of the visceral mass, the pericardium and the adductor muscle.
They are present in the blood spaces actually within the substance of the adductor muscle,
and scattered zooxanthellae were seen in sections of the gills and of the ventral regions
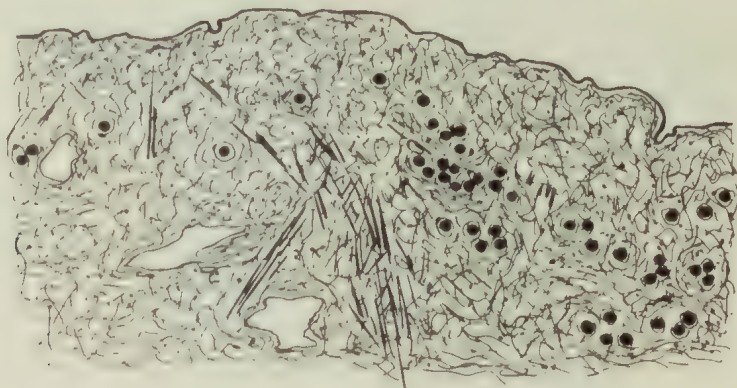
TEXT-FIG. 7. *Hippopus hippopus* : section through portion of exposed dorsal mantle-edge. Fixed
Bouin, stained Delafield's haematoxylin. × 120. Zooxanthellae indicated in black.

of the mantle. Finally (but this matter will be discussed in detail later) vast numbers
of these algae in all stages of digestion are present in phagocytes (Text-fig. 6, P) around
the gut and in between the tubules of the digestive diverticula.

Without exception the zooxanthellae, like those of the corals, are contained within cells
of the animal (Plate V, fig. 11). Brock states the exact opposite, but this was probably
due to faulty fixation of his material (he fixed some specimens in 0·25% chromic acid,
others in dilute osmic and others again in alcohol). My own material consisted of small
entire animals fixed in Bouin, and also of small pieces of tissue from larger animals fixed
in Bouin, Flemming or Carnoy. Sections of this material invariably revealed that the
algae were contained within the blood-cells, the phagocytic powers of which, in other
lamellibranchs, have been previously abundantly demonstrated (Yonge, 1926a, 1926b).
The algae, as shown in Plate V, fig. 11, comprise the entire contents of the cells, the walls
of which are distended to enclose them, the nucleus being pushed to one side and often
compressed. The presence of the algae in these cells explains why it is that they occur
only in the blood-spaces.

Although invariably present, zooxanthellae are by no means so abundant in the
exposed mantle tissues of *Hippopus*. They occur scattered about, as shown in Text-fig. 7,
and are invariably contained within the blood-cells.

7. HYALINE ORGANS IN THE MANTLE OF *TRIDACNA*.

Vaillant (1865) described a series of conical protuberances in the exposed mantle-edges in *Tridacna*, and these he called " tentacules oculiformes ". His examination was confined to dissections and, while admitting the difficulties presented by the thickness and opacity of the tissues, he stated that near the apex of the tubercle there was a spot of pigment which he regarded as a choroid, and associated with this he found a convex transparent capsule resembling a cornea.

Brock (1888) is the only subsequent worker to reinvestigate these structures, which he did by sectioning. He was able to show clearly that, although the protuberances are not in themselves eyes, and there is nothing corresponding to Vaillant's " choroid ", there are, in the protuberances, " some very peculiarly constructed organs of microscopic minuteness, which perhaps might be eyes " (translation by Dallas, 1888). Since, for reasons discussed below, it is highly probable that these organs are intimately concerned with the zooxanthellae, I have studied them carefully in my own sections of *T. crocea*.

(a) STRUCTURE.

As shown in Text-fig. 3, the upper surface of the exposed inner fold of the mantle-edge in *T. crocea*, in common with that of other species of this genus (but not in *Hippopus*), possesses a number of conical projections. These are usually about 1 mm. high (see Text-fig. 8), but taller in the larger species. (Brock speaks of them as at most 2 to 3 mm. wide and of about the same height ; he does not mention which species he studied, but it was larger than *T. crocea*, and *may* have been *T. elongata*.) These protuberances occur, in fully-grown individuals, in a series of rows, while between them and the outer margin of the inner fold of the mantle-edge there are a series of smaller, somewhat scar-like structures which Brock has clearly shown to be developing protuberances.

Within these protuberances or in their precursors are situated lens-like structures, which I propose to call hyaline organs. In *T. crocea*, as shown in Text-fig. 8, I have never found more than one of these in any protuberance, but in the species which he studied, where the protuberances were larger, Brock found as many as twelve, the majority occurring on the outer side (*i. e.* towards the edge of the mantle). In *T. crocea* they have a maximum length of about 0·3 mm. and a maximum breadth of 0·15 mm. ; Brock's figures are 0·2 and 0·15 mm. respectively.

These organs were described by Brock as possessing the " general form of a shallow flask with a broad belly and a short thick neck ". His figures give this general appearance. Here I differ from him. When cut precisely through the long axis they have the form shown in Plate V, fig. 14, namely, an inner rounded body with a thinner neck region and then a smaller outer rounded area, the outermost region being more flattened, although retaining a smooth, convex surface. A misleading impression is frequently obtained from sections not cut in this plane. Each organ is surrounded by a thin but firm capsule of connective tissue with occasional elongate nuclei. The interior is filled with large transparent cells (Plate V, fig. 14, *i.c.*), oval or rounded in shape (Brock described them as polygonal, which he attributed, rightly, to his imperfect fixation), and as much as 20μ or more in diameter. The nucleus is excentric and very small, and the cell boundaries are very well defined ; indeed the general impression is that of a mass of separate cells.

The cells which line the walls of the capsule at the base and around the sides of the inner rounded area are different in character. As shown in Plate V, fig. 14 (*b.c.*), they are attached to the capsular wall, are irregular in shape, stain much more deeply with any cytoplasmic stain and have a larger and central nucleus. They are particularly well developed at the base, where they are very elongated, attaining a maximum length of 30μ, but gradually decrease in size as they extend up the sides of the capsule. Brock noted this " external layer " as he calls it, his views as to its function being mentioned later, but his description, again probably the result of faulty fixation, is somewhat inadequate. I prefer to call this the basal layer, and my sections show clearly that it is from this region that the transparent cells are formed. These are largest in outer regions and smallest at the base of the organs. Those nearest to the basal layer, besides being conspicuously smaller, have frequently a centrally-placed nucleus and rather more deeply staining cytoplasm. Many of the elongated cells of the basal layer are extending into the
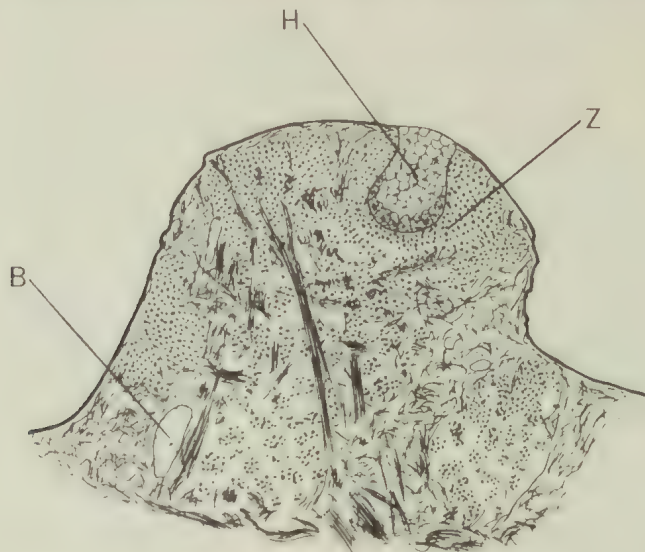
TEXT-FIG. 8. *Tridacna crocea*; section through protuberance on the inner fold of the mantle-edge on the exposed, dorsal side. Fixed Bouin, stained Delafield's haematoxylin. × 57. B, blood-vessel; H, hyaline organ; Z, zooxanthellae around hyaline organ.

cavity, and the general impression gained is that these are cells which will shortly be nipped off and passed into the cavity of the organ, there to increase in size and acquire the transparency and other characteristics of the cells already present. Finally in developing hyaline organs (Plate V, fig. 13) almost all the cells are of this type.

In the fully developed organs the epithelium which covers the capsular wall on the outer surface is very thin, being, as shown in Plate V, fig. 14, reduced either to a thin pavement epithelium, or to a strip of basement membrane little thicker than the underlying capsule. According to Brock this is true of developing organs, but not of the mature ones, over which, according to him, the epithelium, though slightly thinner, is not essentially different from that of the general surface of the inner fold of the mantle-edge. This is certainly not the case in *T. crocea*. Judging from his figures, Brock's statement may be due to the angle at which his sections of the fully-formed organs were cut.

Brock notes, and emphasizes this as a remarkable fact, that he never saw a nerve passing to any of these organs. I am able to confirm this.

Brock discusses at some length the formation of the protuberances, or warts as he

calls them, which Vaillant had considered to be eyes.   He shows that the first stage in formation consists of an inpouching of the epithelium, which he terms a " fosse " (Plate V, figs. 13 and 14, *d*.), on the outer side (*i. e.* nearer to the shell-valves), followed by an elevation on the inner side of this.   Even in the smallest of these he found well-developed hyaline organs, from which he concludes that their formation precedes that of the protuberances.   In my sections of entire young animals (about 8 mm. long after decalcification) there are no protuberances, but there is a single row of hyaline organs (Text-fig. 6, H) near the outer margin of the inner mantle fold.   There is an inpouching on the outer side of this (Plate V, figs. 13 and 14, *d*.), indicating that a protuberance will later be formed.   This is in agreement with Brock's statement that in his smallest specimen (probably of *T. elongata*), with a total mantle length of about 13 cm., he found only a single row, about fifty on each side, of very imperfectly formed warts.

Brock concludes that " during the whole life of the animal new-formation of warts goes on continually, starting from the margin of the mantle ".   This seems to imply that new ones appear in rows nearer to the middle line, but his previous statement, that partially-formed warts are present between those fully formed and the outer margin, indicates that he must have meant the opposite, which is certainly true.   Brock himself failed to find any developing hyaline organs.   In my own sections of young animals I have found abundance of these, as exemplified by Plate V, fig. 13.   In this figure two developing hyaline organs are shown.   The larger (*h.m.*) is roughly spherical, with a diameter of some 80μ.   It is enclosed by a very conspicuous capsule (*c.*) and the cavity contains cells, all but the most central of which are similar to those of the basal layer in fully-formed organs. This organ has not broken through to the surface, being covered by the, as yet unmodified, epithelium, and also by a certain amount of sub-epithelial tissue.   To the outer side the epithelium shows an inpouching (*d.*).   To the outside of this again there is a still smaller hyaline organ (*h.e.*), consisting of little more than a collection of nuclei characteristic of the cells of the basal layer, and round them the much smaller, elongated nuclei of the capsule, the whole being no more than 30μ in diameter.   Beyond this, again, there is another inpouching of the epithelium (*d.*).   There is even evidence, though not decisive, of the formation of yet a third hyaline organ beyond that again.   The ultimate origin of the cells which form the hyaline organs is difficult to determine with any certainty, but sections show that the nuclei of the epithelial cells at the base of the depressions are larger than normal, approximating closely in size and appearance to those of the basal layer in the organs.   There is also some evidence that these may migrate inwards, and that by their subsequent increase there, with the addition of capsular cells, possibly from the surrounding connective tissue, the hyaline organs may originate, their subsequent lens-like character being due to eventual modification of the internal cells.

Hyaline organs are not present in the exposed mantle-tissue of *Hippopus*.

(*b*) FUNCTION.

Brock's work, entirely confirmed in this respect by my own, has shown that Vaillant's description of the protuberances on the mantle as eyes is erroneous.   No retina is present, there is no indication of what Vaillant called a choroid, while, most conclusive of all, the essential sensory nerve of a receptor organ is absent.   Moreover, well-developed pallial eyes are usually confined in the lamellibranchs to actively-swimming genera, such as

Pecten, though light-receptive organs are present in certain of the siphonal tentacles of *Cardium* (Johnstone, 1899 ; Roche, 1925). These consist of a multicellular lens, a retina composed of a single layer of cells and an enclosing sheath. There is a definite nerve connection and there can be no doubt as to their function, particularly as the siphons are the organs most in contact with the environment and are highly sensitive. But in *Tridacna* not only are the animals totally incapable of locomotion, but the mantle-tissues, so far from being sensitive to light, invariably expand to their fullest extent, even in very shallow water exposed to the full force of the tropical sun at noon. Indeed, very considerable mechanical stimulus is needed before they will contract.

Brock came to the somewhat provisional conclusion that the hyaline organs are luminescent. He thought that if the cells of the "external layer" had the power of producing light, the transparent cells might act as prisms. He admitted that he had no knowledge as to the all-important distribution of the pigment (though his sections must have revealed the absence of an enclosing layer of melanin). He quotes an old statement of Rumphius (from his ' Amboinische Rariteitkamer ', Amsterdam, 1705, p. 132) that " they relate many singular things of a large Bia garu [*Tridacna gigas*] which is to be seen in a lagoon of the island Timor Laut, which on opening at night is said to emit a bright light or lustre, which may even be perceived from afar ". But he candidly points out that this, though taken at its face value by Schmidt in Brehm's ' Tierleben ', is only " a pleasant tale of the natives ", adding that the Tridacnidae are so abundant in the whole Indo-Pacific region that it is very unlikely that luminosity, if it existed, would not have been observed. During the thirteen months spent on Low Isles, where literally thousands of *Tridacna* of several species occurred, the various members of the expedition made innumerable night trips on the reef and no luminosity was ever observed in the mantle-tissues of these animals. There remains also the absence of nervous connections, which are just as essential to an effector as to a receptor organ.

I have no doubt personally that the hyaline organs are connected with the presence of the zooxanthellae in the mantle. As shown in Plate V, fig. 14, and in Text-fig. 8, which are in every way typical, the hyaline organs are invariably surrounded with masses of zooxanthellae (this is apparent also in Brock's figures, although he failed to realize its significance). Moreover, the shape of the hyaline organs is such that light received on the gently curved outer surface will be distributed widely in the tissues owing to the much greater curvature of the inner surface. The effect, therefore, will be greatly to increase the effective light-receptive surface, and so the number of algae which can exist within the mantle. This view of the function of the hyaline organs explains the absence of nerves, which is so absolute a bar to any previous explanation.

The origin of these organs is not difficult to understand when one remembers the number of different lamellibranchs in which pallial eyes have, usually independently, appeared : for instance, in *Arca*, *Pectunculus*, *Lima excavata*, *Spondylus*, *Pecten* and *Cardium*. In structure the internal cells of the hyaline organs closely resemble the cells composing the lens in the pallial eyes, and it seems not improbable that both, though in different ways, represent a response to the stimulus of light. The interesting fact is the entirely unique exploitation of this capacity for lens-formation in the mantle by *Tridacna*. But it undoubtedly falls into line with the many other modifications which these animals have undergone as a result, it may confidently be maintained, of their association with zooxanthellae- namely, the manner in which the mantle has twisted round at an angle

of almost 180° to the viscera, so that its free edges face upwards towards the light, and the great thickening of the inner longitudinal fold of the mantle-edge in which the great bulk of the zooxanthellae are contained.

As noted by Brock, the appearance of protuberances is preceded by that of the hyaline organs. This may well be due to the great number of algae which are able to exist in the well-illuminated zone round the hyaline organs. By the automatic removal of waste products of metabolism (carbon dioxide, nitrogenous waste and phosphates), or by the additional supply of oxygen, these may stimulate local growth in the tissues. Such a stimulus to growth has already been postulated in the case of the reef-building corals with their associated zooxanthellae (Yonge, Yonge and Nicholls, Paper No. 8 in this volume; Yonge, 1931). A very interesting confirmation of this is provided by the recent work of Buchsbaum and Buchsbaum (1934), who found that the presence of *Chorella* in tissue cultures of embryonic chick connective tissue and macrophages. and of adult amphibian heart, had a very marked effect, as compared with controls without algae, by stimulating growth. But whether or no the increased numbers of algae present are responsible for the actual formation of the protuberances—which in the species studied by Brock may develop into mushroom-like structures—the formation of these certainly increases the superficial tissues of the exposed regions of the mantle-edge, and so of the number of algae which can be housed in them. It may even be that the vast extent of the exposed mantle-tissues is due. at any rate in part, to the presence of algae within them.

Work on the zooxanthellae of corals (Yonge, Yonge and Nicholls, Paper No. 8 in this volume) indicated that bright light has a detrimental effect on photosynthesis. The possibly deleterious effect of the extremely intense light to which the zooxanthellae of *Tridacna* are frequently exposed may be countered by the intense pigmentation of the tissues, which may be protected themselves in the same way. This is certainly a possible explanation of this pigmentation and also of the much lighter pigmentation in *Hippopus*, where zooxanthellae are less abundant and where hyaline organs are absent.

8. NATURE OF THE ASSOCIATION.

Association between invertebrates and unicellular algae is widespread, but, as recently emphasized (Yonge, 1934). the nature of the association varies widely in different cases. As already shown (Papers 6 8 in this volume), in the reef-building corals the association is essential to the algae, which gain protection and inorganic food, and never exist free in the sea, whereas the corals are. as individuals, able to exist without algae, though these, possibly because they act as automatic organs of excretion and so hasten metabolic processes and promote growth, may be essential to the corals as communities. It was further shown that the zooxanthellae produce large amounts of oxygen during the daytime, though the importance of this to the corals is difficult to assess, and possibly of no great significance.

In the Tridacnidae the nature of the association is obviously different, because, unlike the corals, the animals are, as already shown, definitely specialized for harbouring and actually " farming " the algae. Moreover, the animals, like all lamellibranchs with the exception of the Septibranchia, are herbivorous, and thus capable of digesting the zooxanthellae. The Madreporaria, on the other hand, do not, and, as shown in Report No. 3 in this volume, *cannot* utilize plant material as food.

(a) Influence of Zooxanthellae on Respiration and Excretion.

A series of experiments, similar to those conducted with the corals, were carried out on *Tridacna crocea* to determine whether, in the light, significant amounts of oxygen were produced by the zooxanthellae. Medium-sized animals were selected and placed in large glass jars of about 2800 c.c. capacity. These were filled with sea-water and the tops secured under water. Experiments were run for three-hour periods, first in the light (on the sand behind the aquarium, not in the sea), and then in total darkness. The edges of the shells were broken so that the mantle-edges were exposed even though the shell-valves were closed. Details of the experiment are given in Table I.

TABLE I. *Oxygen Exchange of* T. crocea *after Exposure to Light and Darkness for Three Hours. Oxygen in terms of c.c. per litre.*

No.		Light.				Darkness.		
	Average temperature.	O_2 initial.	O_2 final.	Difference.	Average temperature.	O_2 initial.	O_2 final.	Difference.
A1	20·5 C.	4·91	4·65	0·26	20·5° C.	5·13	4·94	− 0·19
A2	,,	,,	4·59	0·32	,,	,,	4·94	− 0·19
A3	,,	,,	4·14	0·77	,,	,,	4·73	− 0·40
A4	,,	,,	3·26	1·65	,,	,,	2·74	− 2·39
A5	,,	,,	3·30	1·61	,,	,,	4·00	− 1·13
A6	,,	,,	4·67	− 0·24	,,	,,	4·22	− 0·91
A7	,,	,,	4·11	0·80	,,	,,	4·33	− 0·80

Average difference = 0·81.   Average difference = − 0·85.

The results of this experiment, confirmed by others, reveal that no significant amount of oxygen is produced by the zooxanthellae during photosynthesis as compared with the very great amounts which these large animals need for respiration. This is not surprising because, although vast numbers of zooxanthellae are present in *T. crocea*, these are but small compared to the great bulk of the animal tissues. In the corals, on the other hand, the zooxanthellae may nearly equal the animal tissues in bulk.

A series of experiments were next conducted to determine whether or no significant amounts of carbon dioxide were removed during the light and the hydrogen-ion concentration appreciably raised in this way. Experiments were run in a similar manner to those for oxygen, except that the time was increased to $8\frac{1}{2}$ hours. The pH in the water contained in the jar and also in the mantle-cavity was determined colorimetrically. The results are summarized in Table II.

It will be noted that, dealing with average figures, there was a drop of pH 0·29 in the water in the jars after exposure to darkness and a drop of pH 0·22 in the darkness. The difference between the two is probably too small to have much significance, but it indicates that, so far from raising the pH of the water, the removal of carbon dioxide by the zooxanthellae in the light is at any rate balanced by the increased metabolism of the animals. There is, on the other hand, a marked difference in the pH of the water in the mantle-cavity in the two experiments. Although in both cases there is naturally a greater drop here than in the surrounding water, this is significantly less (by pH 0·25) after exposure to light. This is clearly a result of the action of the zooxanthellae. But even after $8\frac{1}{2}$ hours in the darkness the pH in the mantle-cavity in no case dropped below 7·31,

TABLE II.—*Change in pH of Sea-water in Sealed Glass Jars and also in Mantle-cavity of T. crocea at the End of $8\frac{1}{2}$-Hour Periods in Light and then Darkness.*

No.	Light.				Darkness.			
	pH water in jars.		pH in mantle-cavity.		pH water in jars.		pH in mantle-cavity.	
	Initial.	Final.			Initial.	Final.		
1	8·26	7·96	7·83		8·27	8·01	7·76	
2	,,	8·01	7·92		,,	8·01	7·64	
3	,,	8·13	7·82		,,	8·22	7·31	
4	,,	8·18	7·72		,,	8·24	7·46	
5	,,	7·90	7·74		,,	8·02	7·79	
6	,,	7·87	7·75		,,	7·97	7·52	
7	,,	7·65	7·50		,,	7·74	7·42	
8	,,	8·06	7·86		,,	8·19	7·34	
Average		7·97	7·77			8·05	7·53	
Diff. from initial.		0·29	− 0·49			− 0·22	− 0·74	

which is well above the minimum pH in which cilia will act. Here again, therefore, there is no reason for thinking that the animal gains anything of significant value by the removal by the zooxanthellae in light of a certain amount of the carbon dioxide formed by it. The zooxanthellae can only, in short, utilize a very small proportion of the carbon dioxide produced by the animal.

This does not hold true, however, when we come to study the influence of the zooxanthellae on phosphorus excretion (for reasons stated in Paper 6 in this volume it was impossible to study nitrate excretion). Experiments were run with three specimens of *T. crocea* and three of a common species of *Spondylus* of about equal size as representing a typical lamellibranch without algae. The animals were placed in large jars with loosely fitting tops, each containing 2000 c.c. of twice filtered sea-water. The phosphorus content was estimated before the experiment and again at the end of 24 hours. The results are summarized in Table III.

TABLE III.—*Change in Phosphorus Content of Water in Jars Containing Specimens of T. crocea and Spondylus sp.*

Tridacna.	Phosphorus in mgrm. per cubic metre.		Spondylus.	Phosphorus in mgrm. per cubic metre.	
	Initial.	24 hours.		Initial.	24 hours.
1	4·0	0	1	4·0	64·7
2	,,	0	2	,,	109·3
3	,,	0	3	,,	486·4

These figures are very arresting. Whereas in *Spondylus* the phosphorus content of the water was strikingly increased by phosphate excretion, the result of protein katabolism, in *Tridacna* all of this was removed by the zooxanthellae and also the phosphorus originally present in the sea-water. The results are similar to those obtained (Paper 6 in this volume) when the apparent phosphorus excretion of reef-building corals was compared with that of *Dendrophyllia*, which contains no algae, except that the increase in the case of *Spondylus*, as would be expected in view of the much greater amount of animal matter present, is much greater than in that of *Dendrophyllia*. It is clear that

the zooxanthellae automatically remove all phosphorus produced (in the form of phosphates) by the animal, and that, as in the corals, it is probable that the stocks of this, and of other inorganic substances required for protein synthesis, are the limiting factor controlling their abundance.

The very large amount of phosphorus excreted by *Spondylus* of approximately equal size indicates the amount available in *Tridacna crocea*. The zooxanthellae are clearly much better placed than if they remained free in the sea, particularly in the waters of the Barrier Reef, where the nitrogen and phosphorus content is notably low (see Orr, Paper No. 3 in Vol. II of these Reports). In the corals, as already noted, this removal of waste products of protein metabolism may be of the greatest value to the animals, at any rate as members of a community, but is there any evidence that *Tridacna* gains significantly ? There is not the same need for rapid growth in these animals, which, though very abundant, are not obviously more successful (except in ability to attain a large size) than are the other common lamellibranchs of the reef, such as species of *Ostrea*, *Spondylus* or *Pinctada*. In this connection the organs of excretion were examined in view of the fact that in *Convoluta* (Keeble, 1910) the presence of associated algae is correlated with the absence of excretory organs present in other Turbellaria.

So far from being absent, vestigial or even small, the kidneys of all the Tridacnidae are of immense size. In the words of Lacaze-Duthiers, the kidney " est énorme, non seulement parce que l'animal a une grande taille, mais encore parce qu'il prend, dans l'espèce ou le genre, des proportions considérables relativement à la grandeur respective des parties ". Macdonald (1857), one of the earliest observers, was struck by it, and refers to it as " secreting a dark brown fluid loaded with fatty matter ". He was a little uncertain as to its function, thinking that it might " be concerned with the secretion of the byssus ", but, more correctly, suggesting that it might be homologous with the organ of Bojanus.

The great extent of the kidney, which stands out on account of its dark coloration, is shown, in lateral view of the entire animal, in Text-fig. 3 (K), and in cross-section in Text-fig. 6 (K). In the latter the downward extensions are not in the region sectioned, but the union of the kidney sacs of each side, characteristic of the three allied families, Cardiidae, Tridacnidae and Chamidae (Odhner, 1912), is shown. The general morphology of the kidneys has been adequately dealt with by Grobben (1898), Lacaze-Duthiers (1902) and Odhner (1912), the first-named giving a good account also of the pericardial gland (Text-fig. 6, PG). The point of particular interest here is the very great folding of the secreting surface in the sacs, so that the interior of these is almost completely occupied by a spongy mass, as shown in Text-fig. 6. This in turn is filled with numerous yellowish-brown concretions, which give the characteristic colour to the kidneys. These are usually spherical and have a concentric lamellated structure, attaining a diameter of some 25μ. They form almost the sole contents of the kidneys, both cytoplasm and nuclei being usually absent from the cells and even the cell walls being frequently ruptured. In other lamellibranchs small concretions of this character are abundant in the kidney-cells, but in no case, apparently, to the same extent as in the Tridacnidae, the conditions in *Pinna* and *Atrina* (Grave, 1911) being the nearest approach. Similar granules are of widespread occurrence in the Mollusca generally (see Strohl [1914]) for a general account and literature on the subject). There is a possible explanation for their exceptional size and abundance in the Tridacnidae, but this can be most suitably discussed at the end of the next section.

(b) Influence of the Zooxanthellae on Nutrition.

There are good *à priori* reasons for thinking that the Tridacnidae, unlike the corals, may obtain nutriment from the zooxanthellae, because these, like all typical lamellibranchs, feed normally on finely divided food, largely of a vegetable nature. Moreover, it has already been shown that the selective action on the gills and palps is such that only the most minute particles can enter the gut, even those as small as blood-corpuscles of Elasmobranchs (maximum diameter, 14μ) being rejected. Finally, the absorptive and phagocytic surface represented by the tubules of the digestive diverticula is notably reduced. This reduction is clearly indicated in Text-fig. 6, which shows that the place of the diverticula (D) is almost completely taken by masses of phagocytes (P), which everywhere surround them and the various ramifications of the mid-gut (M) and stylesac (S). This figure, however, was drawn from a section near the hind end of the visceral mass, where the diverticula are fewest and the phagocytes most abundant. The diverticula are more numerous around the stomach region, where the phagocytes, though still present in vast numbers, are relatively fewer. But even here the difference between conditions in *T. crocea* and typical lamellibranchs is most striking. This is shown in Text-fig. 9, where a comparison is made between the conditions in *T. crocea* and in *Nucula nucleus* (Protobranch), *Ostrea edulis* (Eulamellibranch) and *Cuspidaria cuspidata* (Septibranch), the drawings being made from my own sections in all cases. In *Nucula* (A) the tubules of the digestive diverticula are small, extremely numerous, and there are very few blood-cells between them. In *Ostrea* (B) the diverticula are more scattered, being embedded in vesicular connective tissue. Blood-cells occur around the tubules, and also around and in the blood-vessels that traverse the matrix of connective tissue. In *Cuspidaria* (D), as in all Septibranchia (owing to their carnivorous habit [Yonge, 1928b]), the tubules are exceptionally wide and blood-cells are practically absent. In *Tridacna* (C) the tubules, which are scattered somewhat like those of *Ostrea*, are surrounded everywhere with a mass of wandering blood-cells.

Examination of these phagocytes under high power reveals that the majority of them contain zooxanthellae. Some of these are apparently intact, but the very great majority are in various stages of digestion, as shown in Plate V, fig. 12. In the early stages of digestion (z.e.) many globules of fat can be seen in Flemming-fixed material, but these disappear in the final stages (z.f.).

There can be no doubt that *Tridacna* consumes great numbers of its zooxanthellae, obtaining a significant amount of food in this way. The zooxanthellae are "farmed" in the mantle edges and other tissues exposed to the light, where they are always intact, and then, when in poor condition or when the animal "needs" them (it is impossible to be certain as to the causal stimulus), they are carried to the visceral mass for digestion. The fact that they are always contained in blood-cells explains alike the means of their transport and of their digestion. The remarkable mobility of the blood-cells in the lamellibranchs, which normally pass into the lumen of the gut and then back, through the epithelium, with ingested food material, has already been shown (Yonge, 1926a and b). Their power of digesting ingested material has also been demonstrated, and this has been confirmed by Takatsuki (1934), who found sucroclastic, lipoclastic and proteoclastic enzymes within them.

The development of this association between the Tridacnidae and zooxanthellae

has been made possible in the first place by the presence of the wandering phagocytic cells characteristic of the lamellibranchs. It is possible, as I have postulated elsewhere (Yonge, 1934), that the original zooxanthellae were those already specialized for life in the carnivorous corals and other Anthozoa (in the same way as Naville [1926] has shown that the zooxanthellae from *Heliactis bellis* may be transferred to the Nudibranch, *Aeolidiella alderi*). This would enable them to live in animal tissues, but even then physiological adaptation would be necessary before they could resist digestion by the phagocytes.
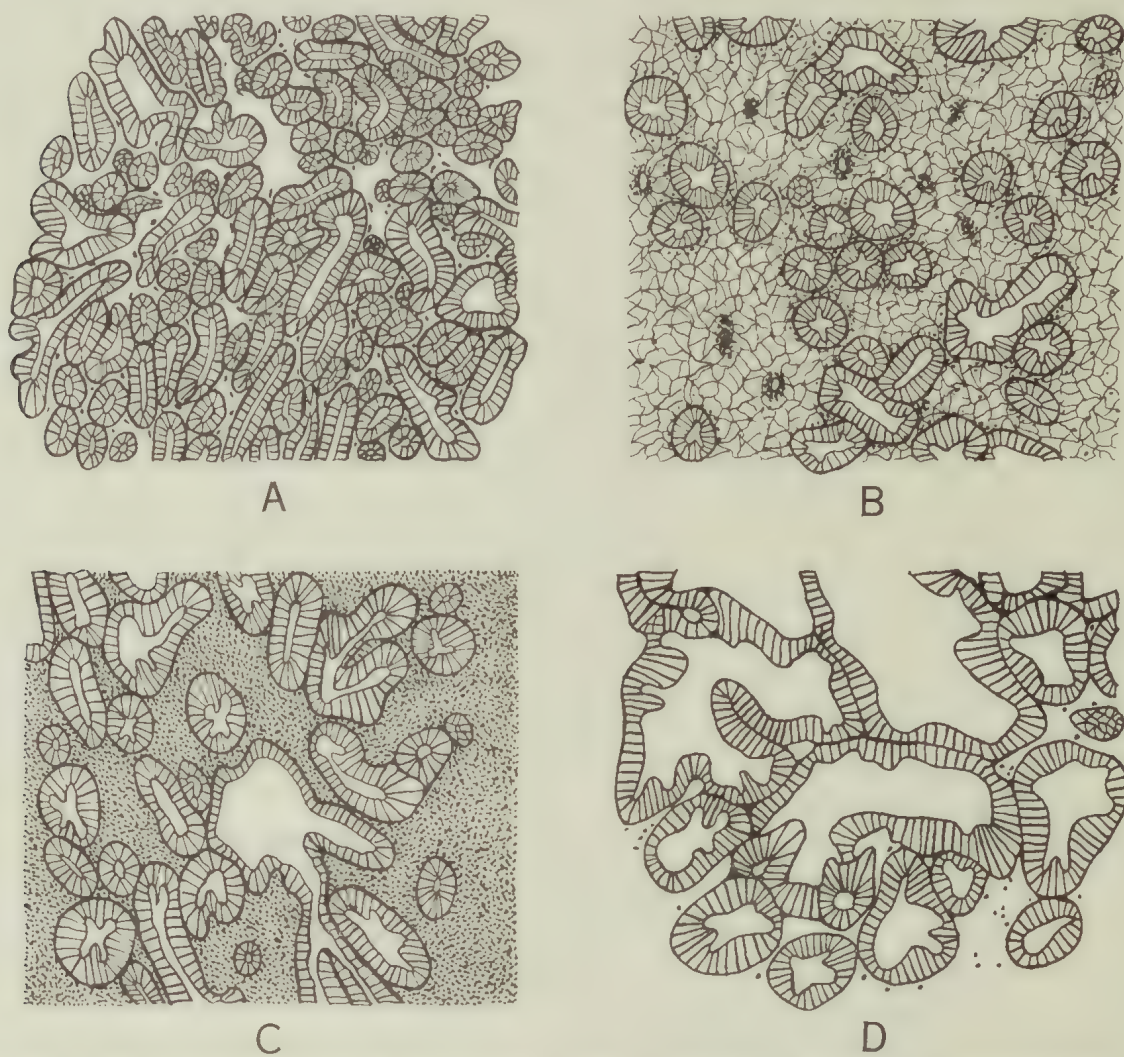
Text-fig. 9. Semi-diagrammatic representation of the digestive diverticula and surrounding tissues in A, *Nucula nucleus*; B, *Ostrea edulis*; C, *Tridacna derasa*; and D, *Cuspidaria cuspidata*. × 72.

As shown elsewhere (Yonge, 1926b), the phagocytes of *Ostrea* ingest and digest diatoms, while I have recently (unpublished work) fed *Ostrea* and *Pecten* with zooxanthellae from *Anemonia sulcata* and found these ingested and digested by phagocytes. In the course of time, the possible sequence of events being described in the next section, the animal evolved its present facilities for " farming " the algae, while these diverged, structurally and physiologically, from the zooxanthellae of the Anthozoa.

The zooxanthellae are presumably carried from the mantle-tissues to the visceral mass by way of the blood-stream. The process is probably rapid, because examination

of fresh blood from the heart of *T. crocea* failed to reveal the presence of zooxanthellae in more than a very few of the numerous blood-cells. The presence, already recorded, of zooxanthellae in the stomach and other regions of the gut, where they are frequently ingested in phagocytes or in the cells of the digestive diverticula, made me suspect originally that the algae were expelled from the surface of the mantle and carried in by the inhalent current. Sections failed to reveal the ejection of algae from the mantle, nor are there ciliary currents leading from the surface of the exposed mantle-tissues to the inhalent opening. Moreover, sections of complete small *T. crocea* (about 1 cm. long) never showed zooxanthellae in the gut or in the cells of the digestive diverticula. Probably, therefore, the zooxanthellae in the gut of the large animals opened had been carried there after the animals had been handled and zooxanthellae liberated by rupturing the tissues.

It is possible that, after digestion by the phagocytes, much of the food is transferred to the cells of the digestive diverticula for storage. Certainly these cells frequently contain numerous fat-droplets. A quantity of indigestible matter must remain, and this, it is suggested, is the explanation of the immense number and large size of the concretions in the kidneys. In a variety of lamellibranchs, such as *Pecten opercularis*, the cells of the digestive diverticula contain masses of yellow concretions, which I have previously described, and concluded to be the indigestible remnants of intracellular digestion (Yonge, 1926a). In this case they are eventually liberated and passed out with the faeces, but in the Tridacnidae, where intracellular digestion takes place primarily in the phagocytes —around, instead of in, the digestive diverticula—this does not occur. Great quantities of minute refractile, greenish-coloured granules are present in the disintegrating zooxanthellae, and this waste matter is presumably eventually carried, by the phagocytes in which the zooxanthellae have been digested, to the kidneys. There it accumulates in the manner already described.

In *Hippopus*, as would be expected in view of the smaller number of algae contained, the digestive diverticula are correspondingly much better developed, and the phagocytes, though still abundant, are much less numerous in the visceral mass. They contain zooxanthellae in all stages of digestion.

In the Tridacnidae association with zooxanthellae is remarkably highly developed— much more so in *Tridacna* than in *Hippopus*. The zooxanthellae are housed and protected, fully exposed to the light, and able to tap at the source abundant supplies of inorganic food, carbon dioxide, nitrogenous excretion and phosphates, though even then the supply of the latter is apparently the limiting factor in *Tridacna*. They are unable to live outside the animal and so are entirely dependent upon it. Unlike the corals and other Anthozoa containing zooxanthellae which are not modified by their presence and are capable of flourishing, as individuals at any rate, in their absence, the Tridacnidae are profoundly modified in structure for the housing and " farming " of the algae. It is impossible, in my opinion, to conceive of them evolving in the absence of this factor, although it might be possible to rid them of zooxanthellae by keeping them in the dark and giving them abundant supplies of extremely minute phytoplankton. Actually one *Hippopus* was found which had grown up half covered by a boulder, and that portion of the mantle in the shade was very pale in colour and contained no zooxanthellae. The Tridacnidae exploit the zooxanthellae by feeding on the surplus, but they are still capable of obtaining some food from the water surrounding them, and so have escaped the fate of *Convoluta roscoffensis* (Keeble, 1910), which loses the power of holozoic nutrition and, by

eventually consuming all of its contained algae, destroys itself. This animal, therefore, exploits the algae to the final destruction of the individual, though not of the race, because eggs are laid before it dies, but in the Tridacnidae the animal exploits the algae still more successfully because, owing to its continued ability to obtain energy from outside sources, only the surplus zooxanthellae are consumed and the individual is never starved. *Tridacna* may be considered the supreme example of the exploitation by an animal of associated algae.

9. EVOLUTION OF THE TRIDACNIDAE.

The discussion on the results of this research resolves itself naturally into a consideration of the manner in which the Tridacnidae have evolved. Lacaze-Duthiers terminates his masterly work on the morphology of *Tridacna elongata* and *Hippopus* with this sentence : " L'animal des Tridacnidés est un Acéphale normal dans toutes ses parties viscérales, seul le manteau et la coquille qu'il produit sont, dans un point de leur étendue, démesurément développés et masquent les dispositions normales que la loi des connexions rétablit." On the basis of the new knowledge contained in this paper it is hoped to elucidate the reasons for this remarkable development and twisting of the mantle, and so of the shell which it secretes, and to outline the principal stages in this process.

The Tridacnidae are, geologically, recent, not occurring earlier than the Eocene. In view of the striking secondary modifications which they have undergone this is not surprising. Unfortunately there are two views as to their place in the classification of the Lamellibranchia. The older view, originally advanced by Lamarck, to which Pelseneer (1906) and Zittel (1927) adhere, associates the Tridacnidae with the Cardiidae and Limnocardiidae in the Sub-Order Cardiacea. A more recent view, originating in Neumayr and upheld by Thiele (1926), places the Tridacnidae with the Carditidae in the Tribe Carditacea. Hedley (1921) supported the latter view, and considers that they evolved from a genus like *Venericardia* by way of elongate forms, such as *V. turgida*, Lamarck (*Cardita incrassata*, Sowerby), and then forms such as *Beguina semiorbiculata* or *Cardita crassicosta*. Hedley, however, considered the hinge to be dorsal, and postulated a mode of evolution resembling that which has produced the monomyarian Filibranchia.* This cannot be accepted. The weight of evidence appears to me to lie with the older view. In structure the gills of the Tridacnidae closely resemble those of the Cardiidae, as Ridewood (1903) has shown, and are quite unlike those of the Carditidae. Odhner (1912) has recorded the resemblance between the kidneys of the Cardiidae and the Tridacnidae. The hinge on which Neumayr's classification is based is not markedly different, except that in *Tridacna* the anterior lateral teeth have disappeared owing to the approximation of the pedal opening to the umbo (the result of the twisting of the mantle), as shown in Plate IV, fig. 9, but the posterior laterals resemble those of *Cardium*. Finally, included in the Cardiidae are *Byssocardium*, Munier-Chalmas, and *Lithocardium*, Woodward, both fossils from the Eocene, which had greatly reduced anterior adductor muscles and bear certain resemblances to *Tridacna*, to which they may have been related.

We will postulate, therefore, that the ancestors of the modern Tridacnidae were animals not unlike the modern *Cardium edule*, with two adductor muscles, a well-developed foot and short siphons projecting at the posterior end. The latter would be the only

---

* Anthony (1920) in a paper seen since this paper was written comes to somewhat similar conclusions. I disagree with him and hope to discuss this matter at more length elsewhere.

parts of the tissues normally exposed to light. We must next postulate an infection of this region by zooxanthellae. These must have been taken in with the food, possibly from damaged Anthozoan planulae, and so ingested—but not, at any rate immediately, digested—by the wandering phagocytic cells, the remarkable development of which in the lamellibranchs has made the association possible. The infection with green algae recorded by Goetsch and Scheuring (1926) in *Anodonta* and *Unio*, although of interest in this connection because the algae are largely confined to the siphonal region, is not a
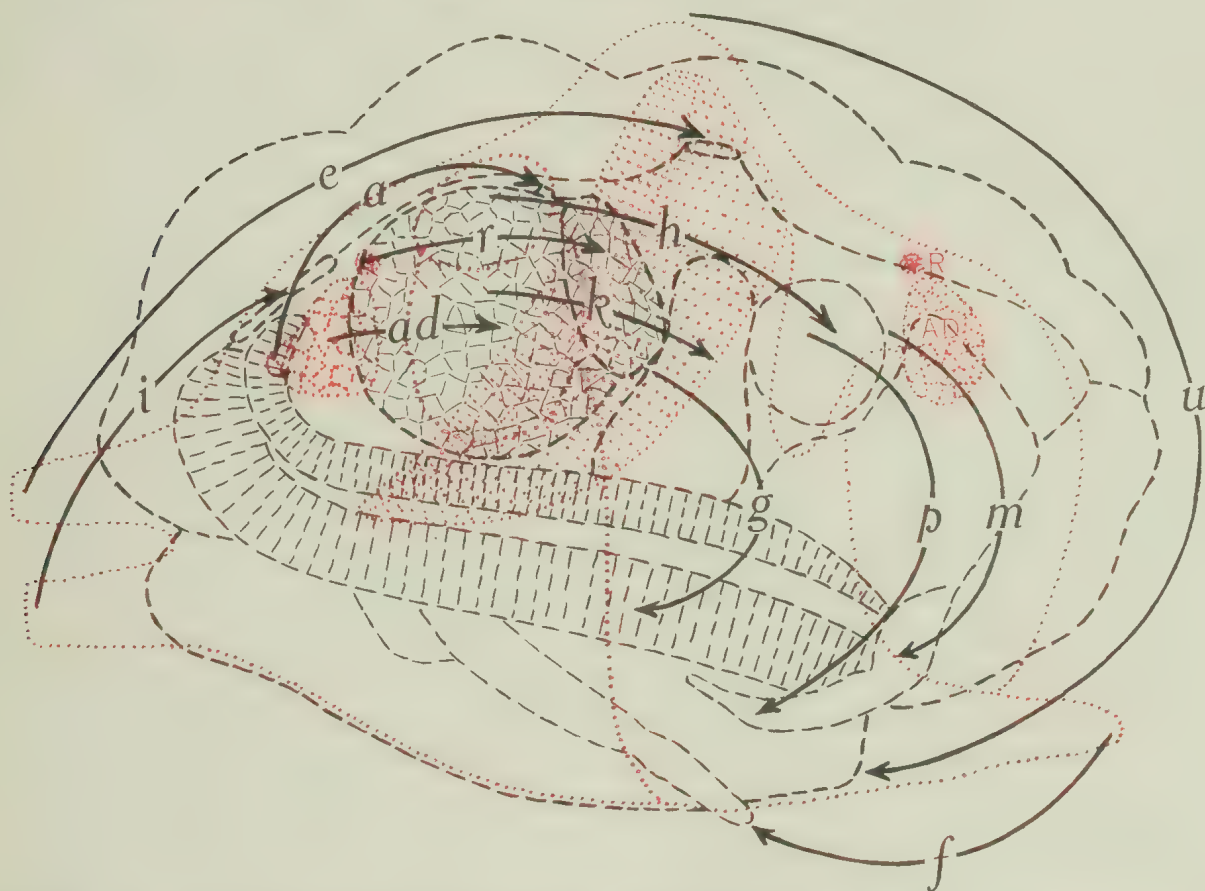
TEXT-FIG. 10.—Diagram indicating the manner in which an animal such as *Cardium edule* (indicated by red dotted lines) may have been converted in *Tridacna crocea* (indicated by broken lines). The turning of the different organs is shown by arrows passing from those of *Cardium* to those of *Tridacna*, each being lettered in the middle. *a.*, anus; *ad.*, posterior adductor muscle; *e.*, exhalent siphon; *f.*, foot; *g.*, inner demibranch of gill; *h.*, heart; *i.*, inhalent siphon; *k.*, kidney; *m.*, mouth; *p.*, labial palps; *r.*, posterior retractor muscle of foot; *u.*, umbo. The anterior adductor muscle (AD) and the anterior retractor muscle of the foot (R) in *Cardium* disappear in the process.

parallel case, because the infection comes *via* the epithelium and the algae are never contained within tissue-cells.

The establishment of zooxanthellae in the siphonal region and the additional supply of food represented by them would clearly render advantageous to the animal any mutation involving a change in form whereby an increased area of mantle-tissue was exposed to the light. We may also consider the possibility, already dealt with, that the zooxanthellae themselves, by promoting the growth of the tissues around them, helped, or possibly initiated, this process. But whatever the cause, the mantle-tissues extended forward along the dorsal side, and the hinge and umbo, as a result, moved forward.

I have endeavoured to display diagrammatically the complete process whereby

Cardium (indicated by red dotted lines) could be converted into *Tridacna* (indicated by broken lines) in Text-fig. 10, the arrows indicating the extent to which the various organs have been displaced. The extension of the mantle-edges along the entire dorsal surface has displaced the umbo (*u.*) from a mid-dorsal position to one approximately one-third of the distance from the anterior end on the ventral side. The siphons have been carried from the posterior to the dorsal surface and widely separated owing to the greater movement of the exhalent (*e.*) than the inhalent (*i.*) siphon. Both have been reduced, particularly the latter, which has become a mere slit in the fused mantle-edges. The posterior adductor muscle (*ad.*) and the posterior retractor of the foot (*r.*) have moved for a short distance forward and increased greatly in size. The anus (*a.*) has moved forward with the posterior adductor, but not to the same extent as the exhalent siphon, so that it is now posterior to this instead of being, as in all other siphonate lamellibranchs, anterior to it. The anterior adductor (AD) and the anterior retractor of the foot (R) have both disappeared as a result of the twisting round of the mantle.* The organs anterior to the posterior adductor, namely, the heart (*h.*) and the kidney (*k.*), have moved forward to much the same extent. The mouth (*m.*) and the palps (*p.*) have moved downward : the movement indicated is possibly greater than has occurred, because in *Cardium edule* they are further to the dorsal side than in many lamellibranchs. This is true also of the gills (*g.*), which in *Cardium* extend almost dorso-ventrally. The position of the gills in *Tridacna* is actually not very different from that in lamellibranchs, such as *Mya*, although some movement has occurred, the anterior end, with the mouth and palps, being more ventrally situated than in other siphonate lamellibranchs, and the posterior end, as a result of the movement of the inhalent siphon with which it is associated, being carried upwards to the posterior end of the dorsal side. Finally, owing to the movement of the hinge, the foot has been pushed for some distance in a posterior direction, although the extension of the pedal gape to the very edge of the cardinal teeth, involving the obliteration of the lateral teeth on that side (originally anterior, now posterior), has reduced this movement to the minimum.

At the same time that this turning of the mantle and shell occurred with the associated secondary effects, the inner fold of the mantle edge increased in width (the velum in other lamellibranchs has arisen in a similar way) and in thickness, and must have acquired (in *Tridacna* but not in *Hippopus*) the capacity to extend laterally beyond the edge of the shell-valves. In this way the content of zooxanthellae was increased, and their powers of multiplication, assuming sufficient food from the excretions of the animal, augmented by greater exposure to light. A further increase would follow the development of the hyaline organs. We may postulate that these arose, a result of the inherent property of exposed mantle tissues to produce lens-like structures, normally associated with eyes, as a response to the stimulus of light. Alternatively we may regard them as modified siphonal eyes of the ancestor (assuming it possessed these, like the modern *Cardium edule*), which have lost retina, nerve and pigment, and retained only the lens, the shape of which has been modified to permit of the greatest possible internal illumination of the tissues. Following this again came the development of protuberances, possible as a direct result of the increase in zooxanthellae around the hyaline organs for reasons already given, with a corresponding further increase in the content of zooxanthellae.

* Unlike the monomyarian Filibranchia and the Ostracea, where this has been caused by an anterior movement of the foot and associated organs.

At the same time the animal became more and more dependent on the zooxanthellae for nutrition. The digestive diverticula decreased in number, their place being taken by the phagocytes which carried the zooxanthellae to the visceral mass for digestion. The feeding organs, gills and palps, though retained in their entirety except where the outer demibranchs are reduced, probably owing to their lessened importance, developed an unusual selective power, so that only the most minute particles were able to enter the gut. Associated changes in the stomach led to the loss of sorting mechanisms in that region. Finally the great amount of excretory matter which accumulated in the phagocytes after digestion of the zooxanthellae led to a great increase in the size of the kidneys and to vast accumulations within them of excretory concretions.

The acquisition of the additional source of nutrition represented by the zooxanthellae, and the " farming " of these, has resulted in changes in the habits of the animals. In the first place they must live in shallow water, as near as possible to the source of light. Thus it is that *Hippopus* and the surface species of *Tridacna* occur always on the upper surfaces of reefs (such as Batt Reef, shown in Plate III, fig. 7), while the others burrow into the beach limestone and the coral rock of the boulder zone on the lee of the reefs (*T. crocea*), or into semi-consolidated shingle of the reef flat (*T. fossor*).

There can be no doubt that the boring habit is secondary in *Tridacna*. Assuming that the ancestors burrowed in sand, as does the modern *Cardium* (which does not, of course, necessarily follow, though I think it is probable), the need for light would explain the change in habit. This would involve the development of the byssus for attachment. It is noteworthy that in *Cardium*, though the byssus gland is normally rudimentary in the adult, it is actually functional in young *C. aculeatum*, and a case of *C. edule* with a functional byssus has been reported (see Johnstone [1899] for references). There can thus be no reason for doubting that the ancestral Tridacnidae were able to acquire a large byssus gland. At the same time as the animals became larger (possibly owing to their now largely sessile life), the foot became smaller. Even at the present time, however, young *T. crocea* possess a well-developed foot by means of which they can move as actively as young *Mytilus*.

During the transition stage, before the hinge had become ventral, the byssus would probably be of the greatest importance in maintaining the animal in such a position that the mantle edges were fully exposed to the light. Indeed the visceral mass would seem to have been anchored by the byssus while the mantle and shell moved round relative to it. After the Tridacnidae evolved their present form and could rest firmly on the broad under-surface of the shell, two lines of evolution can be traced. One led to an increase in size and the ultimate disappearance of the byssus when the weight alone became great enough to ensure stability.* This actually occurs in the life of the individual, *T. derasa* having a byssus and a pedal aperture when small but eventually losing both. In the burrowing forms precisely the opposite takes place. The pedal aperture becomes relatively larger with increasing growth, as Hedley originally observed and figured, and the byssus becomes immense. These species, which never attain any great size, have clung tighter and tighter to the substratum until they have developed the capacity to grind their way into it. Their method of boring downward with the hinge undermost is unique, and *must* have been developed after the modern structure had been attained. *T. fossor*, with

* In these species the underside of the shell became much broader than in the burrowing species. Compare Plate IV, figs. 8 and 9.

its relatively smaller pedal gape and byssus and slighter powers of boring, probably represents an earlier stage in the evolution of this habit than *T. crocea*. The latter has been remarkably successful, having solved better than any other species of *Tridacna* the problem of attachment and protection from an early age. This is proved by its ubiquity, some indication of which is shown in Plate II, fig. 3.

Hippopus we may conceive as having split off from *Tridacna* at some time after the acquisition of zooxanthellae and the turning of the mantle, but before the great development of the inner fold of the mantle-edge and the appearance of hyaline organs. This seems more probable than to assume that it has lost these while retaining the habits of surface species of *Tridacna*. It has not exploited the zooxanthellae to anything like the same extend as *Tridacna*, although they are actually abundant in the mantle-edges which are exposed to the light. It is to be regretted that pressure of work prevented a study of feeding in *Hippopus*. One would expect a less rigorous sorting on the gills and palps, and so more food passed into the gut.

One further point remains for speculation. Is the vast size attained by *T. derasa* due to the association with zooxanthellae ? Thiel (1929) has suggested that the production of oxygen within the tissues by zooxanthellae may assist in the formation of the shell. He has found that lamellibranchs living in well-oxygenated water have thicker shells than those living in water deficient in oxygen. He cites *Tridacna* as an example, but, as stated previously when discussing this matter in reference to corals (Yonge, Yonge and Nicholls, Paper No. 8 in this volume), other lamellibranchs common on the reefs, such as *Chama* or *Spondylus*, which contain no zooxanthellae, have shells just as massive in proportion to their size.* On the other hand, in hot tropical waters, where the metabolic rate is high and the competition amongst plankton-feeders particularly intense, the presence of what I have previously described as " imprisoned phytoplankton " (Yonge, 1931) may well have enabled these animals to attain their present immense size. To a considerable degree they are, with their zooxanthellae, a closed system, and so need far less food from outside than would an animal of the same size which did not possess zooxanthellae. There is only a definite amount of phytoplankton present in the water, and the food current created by the gills certainly cannot increase at the same rate as the demands of the animal with increasing size. There must be a limit to the size of a purely plankton feeder, such as a lamellibranch, and it is quite possible that the possession of associated algae has enabled *T. derasa* to exceed this. It is noteworthy that in this species the outer demibranchs are not reduced.

It is unfortunate that nothing is known of the embryology of the Tridacnidae. It should be possible to follow the turning movement of the mantle and other tissues during development, and also to discover at what stage the zooxanthellae pass from the parent to the young. The Tridacnidae are hermaphrodite ; Grobben (1898) found this in *T. elongata*, and Stephenson (Paper No. 9 in Vol. III of these Reports) in *Hippopus*. It was also discovered that the last-named bred in mid-summer, the majority of those studied spawning rather suddenly in January, though some breeding probably took place from December to March. The spawning period coincided with the temporary absence from

---

* The exceptional thickness of the shell in these genera and in the Tridacnidae is probably correlated with their habitat on the surface of reefs exposed to the full force of the surf. The shell of *T. derasa* and of *Hippopus* is relatively very much thicker about the umbonal region than is that of *T. crocea* ; this may be to provide additional weight for anchoring the animal.

Low Isles of the investigators concerned. so that no embryos were obtained. A series of seventeen artificial fertilizations were undertaken by Mrs. Stephenson without a completely normal result. She thinks this may have been due to unripeness of the eggs in the earlier fertilizations and to the high temperatures in the later ones. But it seems possible that the absence of zooxanthellae may have been responsible ; these do not appear in her figures of sections of mature gonads, and possibly are carried into the eggs immediately before these are extruded, and are an essential factor in normal development.

Although the foregoing account of the possible mode of evolution of the Tridacnidae cannot, as yet, be confirmed by embryological data, it is advanced as a working hypothesis. It does not postulate any intermediate stages conceivable morphologically but functionally impossible, while in the original acquisition of the zooxanthellae and the exploitation of these there lies a functional reason for the changes which have undoubtedly taken place.

10. SUMMARY.

1. The Tridacnidae are amongst the most conspicuous members of the fauna of coral reefs in the Indo-Pacific region.

2. They are unique amongst Lamellibranchia in two respects : the relation of the mantle and shell to the other organs and the universal presence of zooxanthellae in the tissues.

3. They may be divided into two groups according to the mode of life. *T. derasa*, *T. elongata*, *T. mutica*, *T. squamosa* and *Hippopus hippopus* are surface-living species, while *T. crocea* and *T. fossor* are boring species.

4. The surface-living species lose the byssus during growth and the pedal opening in the shell gradually closes. They are eventually maintained in position by weight alone, resting on the hinge and umbo. which are ventral instead of dorsal. One of these species, *T. derasa*, may attain a length of $4\frac{1}{2}$ ft., and is the largest lamellibranch ever evolved.

5. *T. crocea* bores into coral boulders until the edges of the shell valves lie flush with the surface of the rock ; *T. fossor* occurs embedded in partially consolidated coral fragments.

6. All boring species have a wide pedal aperture which increases, relatively as well as absolutely, with age.

7. Young *T. crocea* (1–2 cm. long) attach themselves by means of a byssus in holes on the surface of boulders or beach limestone. They possess an extensible foot and can move actively, crawling up surfaces with the additional aid of temporary byssus threads.

8. The assumption of the boring habit involves a progressive increase in the size of the byssus and pedal opening, and a progressive reduction in the size of the foot.

9. Boring is entirely mechanical. A firm purchase is obtained by means of the exceptionally stout byssus, and the animals grinds its way downward by rocking both laterally and longitudinally. The shells of adults are ridged near the free, dorsal surface, but this has worn away over the ventral region which is responsible for boring. The differential growth of the shell and the oblique entrance of the animal enable the byssus attachment to be pushed towards the posterior end as burrowing proceeds, and prevent undercutting of the point of attachment. The animal is ultimately imprisoned in the burrow. This mode of boring is unique.

10. The structure and functions of the feeding organs, gills and palps do not differ fundamentally from those of other lamellibranchs. In *T. crocea* and *Hippopus* (but not in *T. derasa*) the outer demibranch is reduced to a single lamella. The nature of the feeding currents is described.

11. Selective action on the gills and palps is very highly developed, particles 14μ in diameter being rejected. Correlated with this is the small size of the mouth and absence of sorting mechanisms in the stomach, the anatomy and ciliary currents of which are described.

12. The structure of the alimentary canal is described. Assimilation and intra-cellular digestion take place in the digestive diverticula (which are greatly reduced in number) and also in the phagocytic blood-cells, which may pass into the lumen of the gut.

13. Very little food was found in the gut apart from zooxanthellae, which may have entered when the animals were opened.

14. Immense numbers of zooxanthellae invariably occur in the Tridacnidae. They are deep brown and spherical, with an average diameter of about 7μ. A cellulose wall cannot be detected. The nucleus is larger than that of zooxanthellae from corals, and the pyrenoid smaller, while, unlike these, starch is present, as well as oil-droplets. Division stages are of frequent occurrence. Sexual stages do not occur.

15. The zooxanthellae are housed primarily in the inner lobes of the mantle-edges on the dorsal side. These, in *Tridacna*, extend far over the free edges of the shell-valves in life, forming a broad, upwardly directed sheet of highly pigmented tissue, always fully exposed to the light. In *Hippopus* the mantle-edges do not extend in this way, but the shell valves open to a greater extent than in *Tridacna*.

16. The zooxanthellae are confined to the blood-sinuses and are invariably contained within amoeboid blood-cells. The Tridacnidae literally " farm " the algae in their greatly enlarged mantle-edges.

17. The inner, upwardly-directed surface of the inner lobe of the dorsal mantle-edge in *Tridacna* contains a number of conical protuberances. These are not eyes, but carry lens-like structures, here termed hyaline organs.

18. These consist of an inner rounded body, a thinner neck region and an outer, smaller rounded area, the free surface having a smooth, convex surface over which the mantle epithelium is greatly reduced. They are surrounded with a capsule of connective tissue, and filled with transparent cells derived from a basal layer of more deeply staining cells. Nerves are always absent.

19. The formation of hyaline organs, the development of which is described, always precedes that of the protuberances.

20. The hyaline organs are neither eyes nor luminous organs, as previously conjectured, but the means whereby the internal illumination of the mantle-tissues is increased for the benefit of the zooxanthellae. They are always surrounded by great numbers of these algae.

21. The increase in the zooxanthellae possibly stimulates local growth in the tissues, and so causes the formation of protuberances.

22. Experiments failed to reveal any significant production of oxygen or removal of carbon dioxide by the zooxanthellae in the light. On the other hand, the algae automatically remove *all* the phosphorus excreted by the animal and even the phosphorus present in the water around. This may be the limiting factor controlling their abundance.

23. In *Tridacna* the visceral mass contains vast numbers of phagocytic blood-cells, which surround the reduced digestive diverticula and other regions of the gut. They contain zooxanthellae in all stages of digestion. In *Hippopus* there are fewer of these, correlated with the smaller content of zooxanthellae in the mantle-tissues.

24. The zooxanthellae are carried from the mantle in the phagocytes. *Tridacna*, and to a less extent *Hippopus*, consumes great numbers of its zooxanthellae, so obtaining significant amounts of food.

25. The indigestible material remaining in the phagocytes is presumably carried to the kidneys, and this explains both the abnormal size of these and the presence within them of great numbers of large concretions.

26. The Tridacnidae are profoundly modified for the housing and final digestion of the zooxanthellae. *Tridacna* may be considered the supreme example of the exploitation of associated algae by an animal. Unlike *Convoluta roscoffensis*, it never loses the power of holozoic nutrition, and so only the surplus zooxanthellae are consumed.

27. The Tridacnidae are geologically recent. They probably evolved from the same stock as the modern Cardiidae. The possible course of evolution is outlined.

28. The probable original establishment of zooxanthellae in the siphonal region would render advantageous any dorsal extension of the mantle-tissues. This involved the twisting round of the mantle, the final displacement of the umbo and hinge to the ventral side, and the displacement of other organs to a greater or less extent, while the anterior adductor and pedal retractor disappeared.

29. This was accompanied by an increase in the exposed mantle-edges, appearance of hyaline organs (in *Tridacna*), and the increasing dependence of the animals for food on the zooxanthellae with a correlated reduction in the digestive diverticula (and gills except in *T. derasa*).

30. The resultant changes in the habits of the Tridacnidae are described. The assumption of the boring habit must have followed the twisting of the mantle and shell.

31. The presence of associated algae may have enabled the Tridacnidae to exceed the limits normally set to the size of a plankton feeder and so be responsible for the immense size attained by *T. derasa*.

11. REFERENCES.

ANTHONY, R. 1920. L'interprétation du type morphologique de la Tridacne et de l'Hippopus. Bull. Soc. Sci. Ouest, Nantes, (3), VI, pp. 99 107, text-figs. 1–3.

BLAINVILLE, H. M. D. de. 1825. Manuel de Malacologie et de Conchyliologie. Paris, pp. viii, 664.

BOSCHMA, H. 1924. On the Food of Madreporaria. Proc. Acad. Sci. Amsterdam, XXVII, pp. 13–23, text-figs. 1, 2.

Boycott, A. E. 1926. A Green Alga Parasitic in a Water Snail. North Western Nat. I, pp. 10-11, pl. i.

Brandt, K. 1883. Über die morphologische und physiologische Bedeutung des Chlorophylls bei Thieren. Mitt. Zool. Stat. Neapel, IV, pp. 191-302, pls. xix, xx.

Brock, J. 1888. Über die sogenannten Augen von *Tridacna* und das Vorkommen von Pseudochlorophyllkörpen im Gefasssystem der Muscheln. Z. wiss. Zool. XLVI, pp. 270-288, pl. xxii. (English translation by W. S. Dallas, in Ann. Mag. Nat. Hist. (6), I, pp. 435-452.)

Buchsbaum, R., and Buchsbaum, M. 1934. An Artificial Symbiosis. Science, LXXX, pp. 408-409.

Clessin, S. 1873. Beiträge zur Molluskenfauna der Oberbayerischen Seen. KorrespBl. Zool.-Min. Ver. Regensburg, 1873, xxvii, pp. 56- .

Fedele, M. 1926. Sulle Strutture e Funzione bei Ciechi Epatopancreatici nei Molluschi Opistobranchi. Boll. Soc. Biol. Sper. I, fasc. 4, pp. 1-5.

Goetsch, W., and Scheuring, L. 1926. Parasitismus und Symbiose der Algengattung *Chlorella*. Z. Morph.Ökol. Tiere, VII, pp. 221-253, text-figs. 1-15.

Graham, A. 1931. On the Morphology, Feeding Mechanisms, and Digestion of *Ensis siliqua* (Schumacher). Trans. Roy. Soc. Edinb. LVI, pp. 725-751, pl. i, text-figs. 1-8.

Grave, B. H. 1911. Anatomy and Physiology of the Wing-shell, *Atrina rigida*. Bull. U.S. Bur. Fish. XXIX, pp. 409-439, pls. xlviii-l, text-figs. 1-15.

Grobben, C. 1898. Beiträge zur Morphologie und Anatomie der Tridacniden. Zoologische Ergebnisse der Expedition S.M.S. " Pola ", Denkschr. Akad. wiss. Wien, LXV, pp. 433-444, pls. i-iii.

Haffner, K. v. 1925. Untersuchungen über die Symbiose von *Dalyellia viridis* und *Chlorohydra viridissima* mit Chlorellen. Z. wiss. Zool. CXXVI, pp. 1-69, pl. i, text-figs. 1-27.

Hecht, E. 1895. Contribution à l'étude des Nudibranches. Mem. Soc. zool. France, VIII, pp. 539-711, pls. i-v.

Hedley, C. 1921. A Revision of the Australian *Tridacna*. Rec. Aust. Mus. XIII, pp. 163-172, pls. xxvii-xxxiv, text-fig. 1.

Henneguy, L.-F. 1925. Contribution à l'histologie des Nudibranches. Arch. Anat. Micr. XXI, pp. 400-468, pl. v, text-figs. 1-30.

Hornell, J. 1909. A Note on the Presence of Symbiotic Algae in the Integuments of Nudibranchs of the Genus *Melibe*. Rpt. Mar. Zool. Okhamandal, I, pp. 145-148, text-figs. 1-9.

Johnstone, J. 1899. Cardium. L'pool. Mar. Biol. Comm. Mem. No. II, pp. 84, 6 pls., 1 map.

Keeble, F. 1910. Plant-Animals : A Study in Symbiosis. Cambridge, pp. viii, 163, pl. i, figs. 1-22.

Lacaze-Duthiers, H. de. 1902. Morphologie de *Tridacna elongata* et de *Hippopus*. Arch. Zool. Exp. Gén. (3), X, pp. 99-212, pls. i-x.

Macdonald, J. D. 1857. On the Anatomy of *Tridacna*. Proc. R. Soc. VIII, pp. 589-590.

Naville, A. 1926. Notes sur les Eolidiens. Un Eolidien d'eau saumâtre. Origine des nématocystes. Zooxanthelles et homochromie. Rev. Suisse Zool. XXXIII, pp. 251-289, text-figs. 1-9.

Negri, A. de, and G. de. 1876. Farbstoffe aus *Elysia viridis*. Ber. dtsch. chem. Ges., IX Jahrg., p. 84.

Nelson, T. C. 1918. On the Origin, Nature, and Function of the Crystalline Style of Lamellibranchs. J. Morph. XXXI, pp. 53-111, text-figs. 1-17.

Odhner, N. 1912. Morphologische und phylogenetische Untersuchungen über die Nephridien der Lamellibranchien. Z. wiss. Zool. C, pp. 287-391, text-figs. 1-40.

Pelseneer, P. 1906. A Treatise on Zoology. Edited by E. Ray Lankester. Part V : Mollusca. London, pp. 355, figs. 1-301.

Quoy and Gaimard. 1834. Voyage de decouvertes de l'Astrolabe, 1826-29. Zoologie, III, Paris, pp. 1-954.

Ridewood, W. G. 1903. On the Structure of the Gills of the Lamellibranchia. Phil. Trans. B, CXCV, pp. 147-284, text-figs. 1-61.

Roche, W. L. 1925. Note on the Microscopic Anatomy of the Tentacular Sense Organ of *Cardium edule*. J. R. Micr. Soc. 1925, pp. 154-158, text-figs. 1-6.

Strohl, J. 1914. Die Exkretion bei den Mollusken. Handb. vergl. Physiol., H. Winterstein, II, 2, pp. 443-607, text-figs. 61-107.

Takatsuki, S. 1934. On the Nature and Functions of the Amoebocytes of *Ostrea edulis*. Quart. J. Micr. Sci. LXXVI, pp. 379-431, text-figs. 1-12.

Tamura, T. 1931. The Power of the Adductor Muscle of the Lamellibranchs Inhabiting in the South Sea Islands. Sci. Rpt. Tôhoku Univ., 4th ser., VI, pp. 348-390, text-fig. 1.

Thiel, M. E. 1929. Zur Frage der Ernährung der Steinkorallen und der Bedeutung ihrer Zooxanthellen. Zool. Anz. LXXXI, pp. 295-305.

Thiele, J. 1926. Bivalvia-Muscheln. Handbuch der Zoologie, Kükenthal and Krumbach, V, pp. 161-198, text-figs. 246-294.

VAILLANT, L. 1865. Recherches sur la Famille des Tridacnides. Ann. Sci. nat., Zool. (5), IV, pp. 65–172, pls. viii–xii.

WOODWARD, S. P. 1855. Descriptions of the Animals of Certain Genera of Bivalve Shells. Ann. Mag. Nat. Hist. (2), XV, pp. 99–101, text-figs. 1–4.

YONGE, C. M. 1923. The Mechanism of Feeding, Digestion and Assimilation in the Lamellibranch *Mya*. Brit. J. Exp. Biol. I, pp. 15–63, text-figs. 1–27.

—— 1926a. The Digestive Diverticula in the Lamellibranchs. Trans. Roy. Soc. Edinb. LIV, pp. 703–718, pls. i, ii.

—— 1926b. Structure and Physiology of the Organs of Feeding and Digestion in *Ostrea edulis*. J. Mar. Biol. Ass. U.K., n.s. XIV, pp. 295–386, text-figs. 1–42.

—— 1928a. Feeding Mechanisms in the Invertebrates. Biol. Rev. III, pp. 21–76, text-figs. 1–25.

—— 1928b. Structure and Function of the Organs of Feeding and Digestion in the Septibranchs, *Cuspidaria* and *Poromya*. Phil. Trans. B, CCXVI, pp. 221–263, pls. xii–xiv, text-figs. 1–7.

—— 1931. The Significance of the Relationship between Corals and Zooxanthellae. Nature, London, CXXVIII, pp. 309–310.

—— 1932a. Giant Clams and Burrowing Clams. Nat. Hist. N.Y. XXXII, pp. 244–257, text-figs. 1–20.

—— 1932b. On the Size Attained by the Crystalline Style in *Tridacna* and *Strombus*. Proc. Malac. Soc. Lond. XX, pp. 44–45.

—— 1934. Origin and Nature of the Association between Invertebrates and Unicellular Algae. Nature, London, CXXXIV, pp. 12–13.

ZIRPOLO, G. 1923. Richerche sulla simbiosi fra Zooxanthelle e *Phyllirrhoe bucephala* Peron et Leseur. Boll. Soc. Nat. Napoli, XXXV, pp. 129–138.

ZITTEL, K. A. v. 1927. Text-book of Palæontology. Edited by C. R. Eastman. 2nd Edition. Vol. I. London, pp. x, 839, figs. 1–1594.

DESCRIPTION OF PLATE I.

Fig. 1.—*Tridacna derasa*; photograph of an individual a little over 3 ft. long when partially uncovered at low tide. The great thickness of the mantle-edges prevents the shell valves from completely closing. This animal lived on the surface of the reef off Michaelmas Cay.

Fig. 2. *Tridacna derasa*; photograph, taken from directly overhead, of an individual, 14 in. long, which was fully expanded and just covered with water. The inhalent aperture is closed and the exhalent aperture wide open. This animal lived in a small pool on the reef flat at Low Isles.
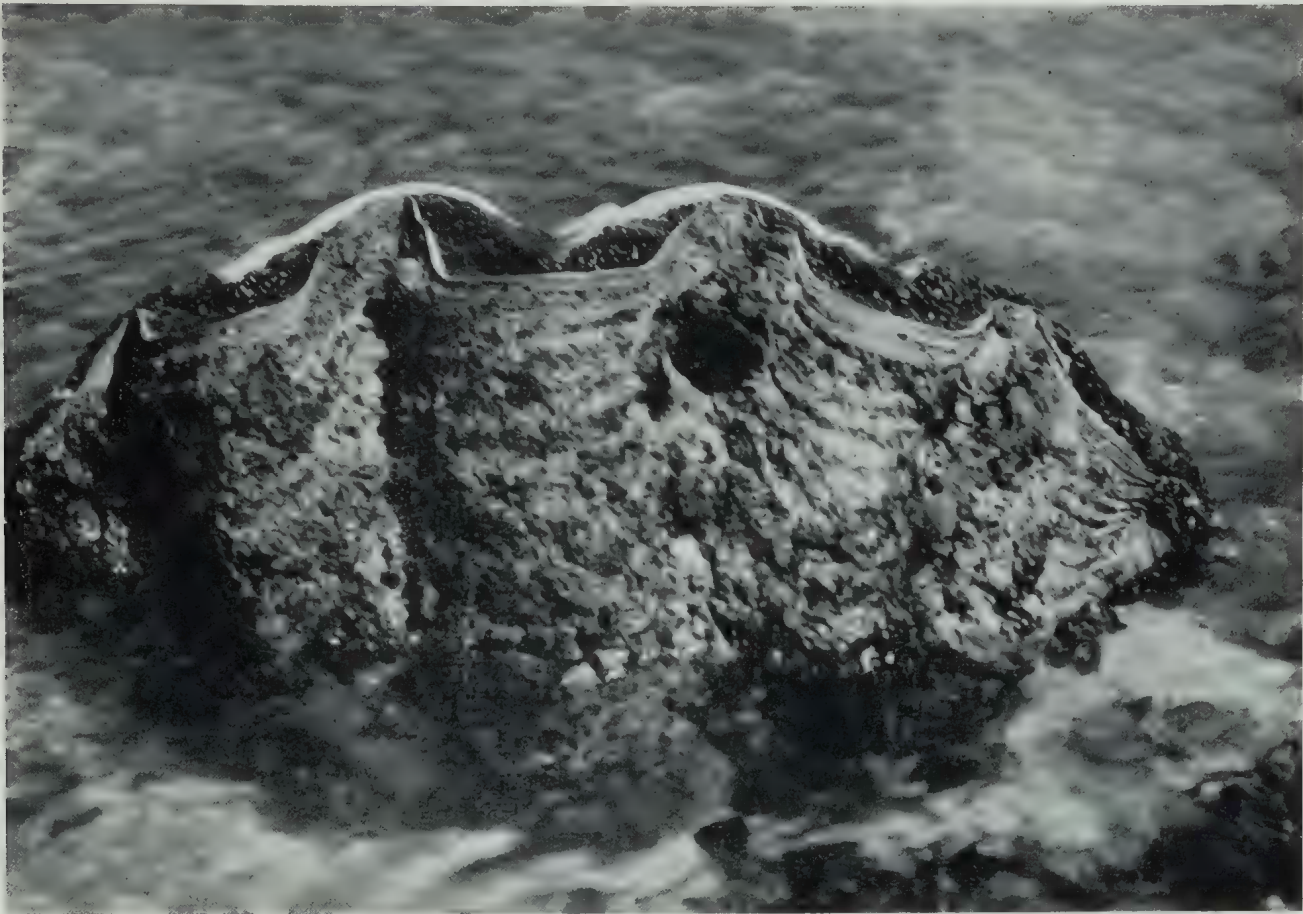
GREAT BARRIER REEF EXPEDITION 1928-29.

Brit. Mus. (Nat. Hist.).   REPORTS, VOL. I, No. 11.   PLATE I.

Photo M. J. Yonge.]   FIG. 1.

Photo M. J. Yonge.]   FIG. 2.   [Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE II.

Fig. 3. *Tridacna crocea*; photograph of a boulder of coral rock exposed at low tide and containing twelve animals which had burrowed into it. The mantle-edges have been withdrawn, but complete closure of the shell is impossible. Low Isles reef.

Fig. 4. *Tridacna crocea*; photograph taken from above of an individual just covered with water and with fully expanded mantle-edges. The inhalent and exhalent apertures are both conspicuous and fully open. The protuberances on the mantle-edge are shown. Low Isles reef.
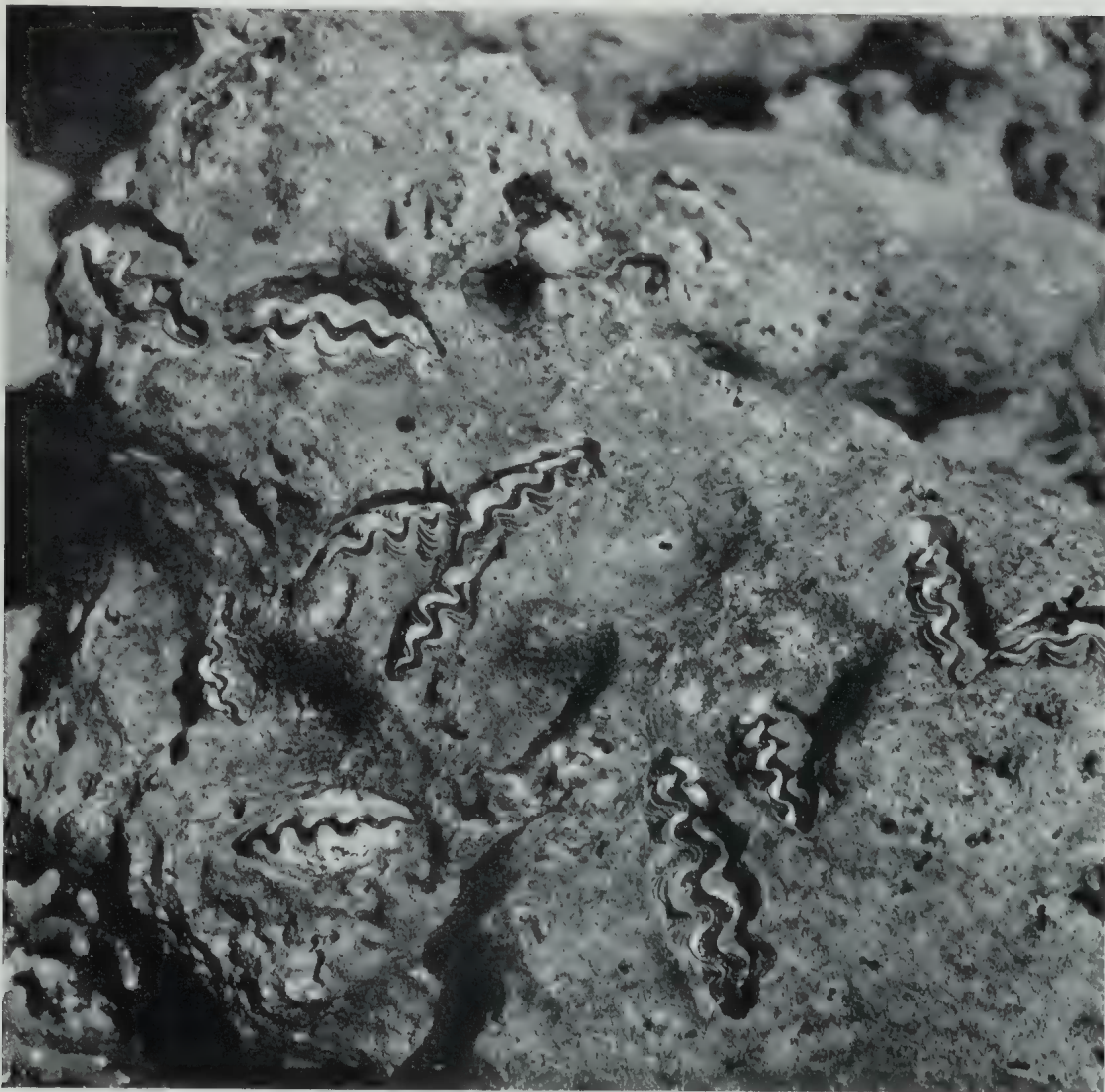
GREAT BARRIER REEF EXPEDITION 1928 29.

Brit. Mus. (Nat. Hist.).   REPORTS, VOL. I, No. 11.   PLATE II.

Photo M. J. Yonge.   FIG. 3.

Photo C. M. Yonge.   FIG. 4.   Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE III.

Fig. 5. *Tridacna crocea*; photograph of an individual which has made a burrow in the dead area in the middle of a living coral colony, exposed at low tide. Low Isles reef.

Fig. 6. *Hippopus hippopus*; photograph, taken from the posterior end, of a fully expanded individual just covered with water. The great extent of the exposed mantle-edges, which in this genus do not extend over the edge of the shell valves, is shown, also the widely open inhalent aperture. Low Isles reef.

Fig. 7. Photograph of the surface of Batt Reef when exposed at low-water spring tides. Such an area forms the typical habitat of *Hippopus hippopus*, several specimens of which are shown in the foreground, of *T. derasa*, and of the other surface-living species of *Tridacna*.

GREAT BARRIER REEF EXPEDITION 1928-29.

Brit. Mus. (Nat. Hist.). REPORTS, VOL. I, No. 11. PLATE III.

Photo T. C. Roughley.] FIG. 5.

Photo T. C. Roughley.] FIG. 6.

Photo G. W. Otter. FIG. 7. [Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE IV.

Fig. 8.- *Hippopus hippopus* ; photograph of the underside of the shell showing the hinge and the absence of a pedal aperture (shell valves slightly separated to show the exact interdigitation).   × $\frac{2}{3}$.

Fig. 9.--*Tridacna crocea* ; photograph of the underside of the shell showing the hinge and the extensive pedal aperture.   × $\frac{3}{4}$.

Fig. 10.- *Tridacna crocea* ; lateral view showing the absence of projecting ridges on the under, grinding surface of the shell valves and their presence nearer the upper, free surface.   × $\frac{3}{4}$.

GREAT BARRIER REEF EXPEDITION 1928–29.

Brit. Mus. (Nat. Hist.).   REPORTS, VOL. I, No. 11.   PLATE IV.
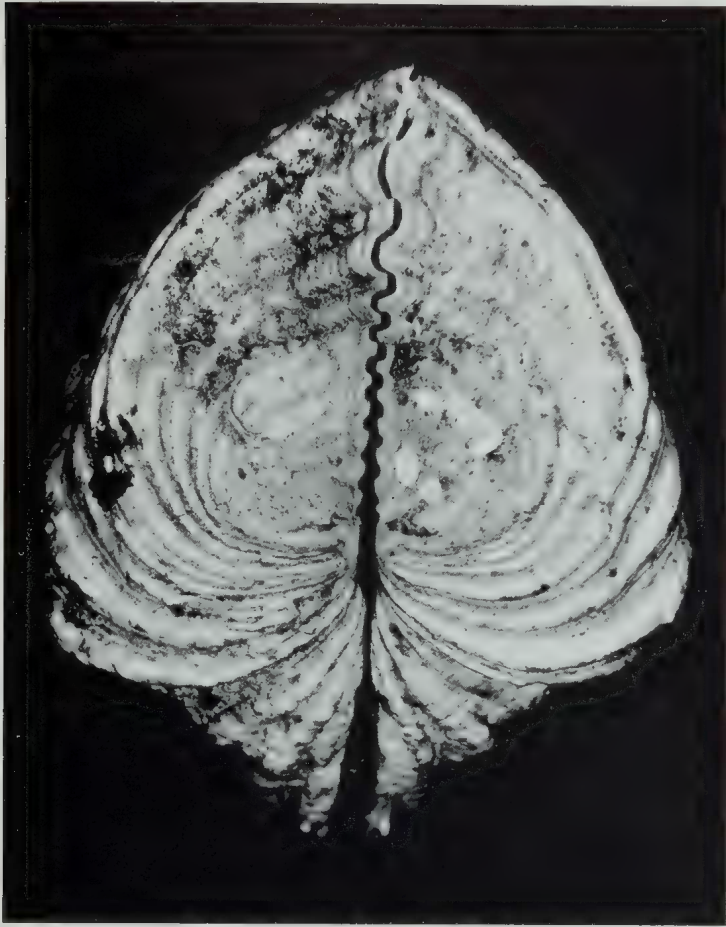
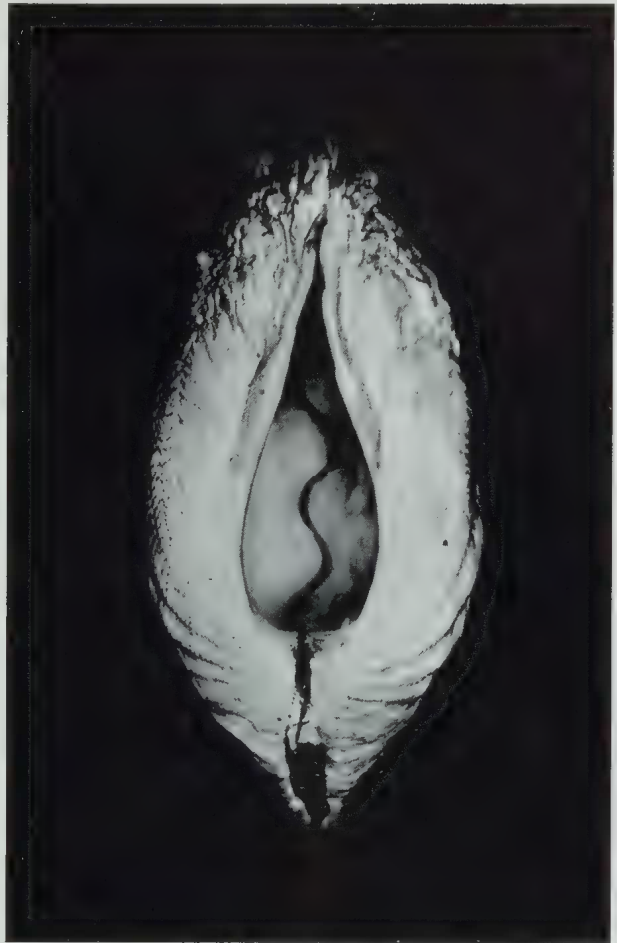*Photo M. W. Harris.)*   FIG. 8.

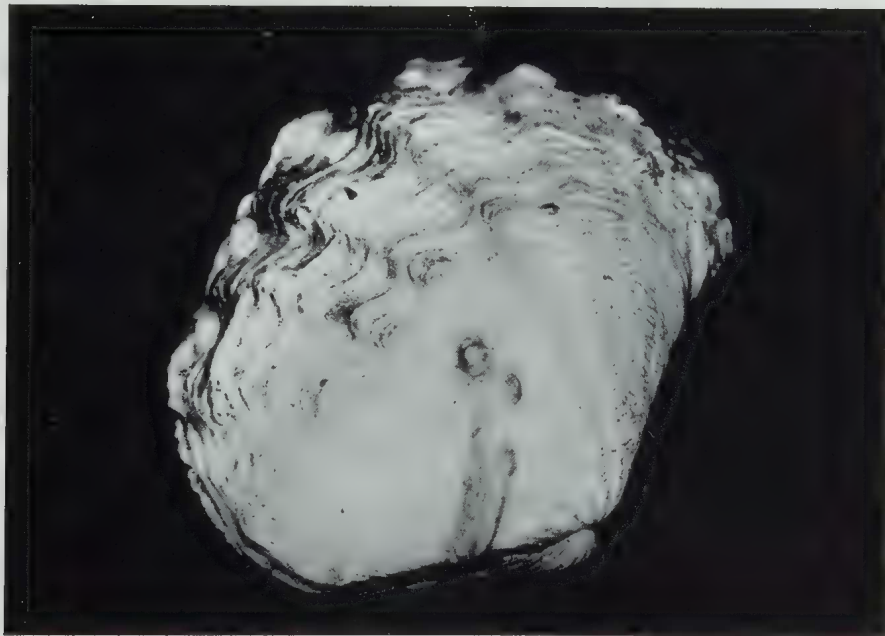*Photo M. W. Harris.*   FIG. 9.

Photo M. W. Harris.   FIG. 10.   *Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE V.

Lettering employed : *b.*, blood-vessel ; *b.c.*, basal layer of darkly-staining cells in the hyaline organs ; *c.*, capsular wall around hyaline organ ; *c.p.*, cell-wall of phagocytic blood-cell ; *c.t.*, connective tissue ; *d.*, depression (" fosse ") in epithelium of mantle on outer side of hyaline organ ; *e.*, epithelium of mantle ; *f.*, fat ; *h.e.*, hyaline organ in very early stage of development ; *h.m.*, hyaline organ in medium stage of development ; *i.c.*, internal layer of transparent cells in the hyaline organs ; *n.p.*, nucleus of phagocyte ; *n.z.*, nucleus of zooxanthella ; *o.h.*, outer surface of hyaline organ ; *p.*, pyrenoid of zooxanthella ; *p.c.t.*, phagocyte in connective tissue ; *z.*, zooxanthellae around hyaline organs ; *z.e.*, zooxanthella in early stage of digestion within phagocyte ; *z.f.*, zooxanthella in final stage of digestion within phagocyte.

FIG. 11.   *Tridacna crocea* ; section through inner fold of the dorsal mantle edge.   Fixed in Bouin's fluid, stained iron-haematoxylin.   8μ.   1250.

FIG. 12.   *Tridacna crocea* ; group of phagocytic blood-cells around the digestive diverticula and containing zooxanthellae in various stages of digestion.   Fixed Flemming's strong fluid, stained safranin and light green.   6μ.   1250.

FIG. 13.   *Tridacna crocea* ; section through inner fold of the dorsal mantle edge of a young individual (8 mm. long after decalcification) showing an early and a medium stage in the development of hyaline organs.   Fixed Bouin's fluid, stained Delafield's haematoxylin and eosin.   8μ.   × 180.

FIG. 14.   *Tridacna crocea* ; section through inner fold of the dorsal mantle edge of an adult individual showing a fully developed hyaline organ surrounded by great numbers of zooxanthellae.   Fixed Flemming's strong fluid, stained Mann's methyl blue and eosin.   6μ.   × 180.

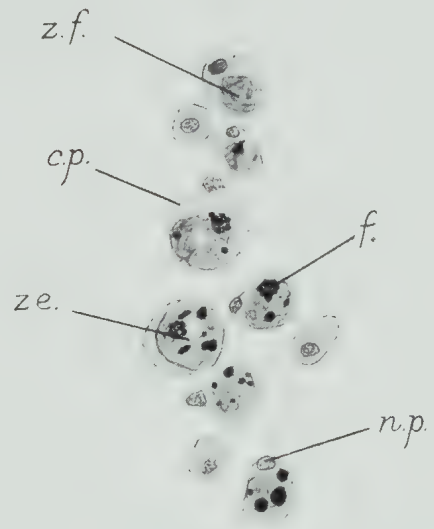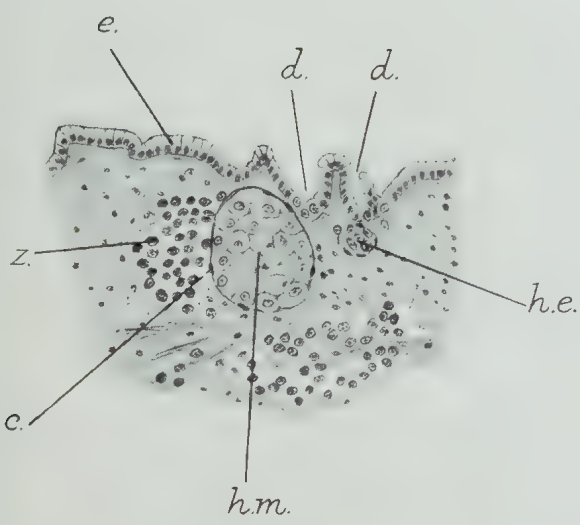GREAT BARRIER REEF EXPEDITION 1928-29.
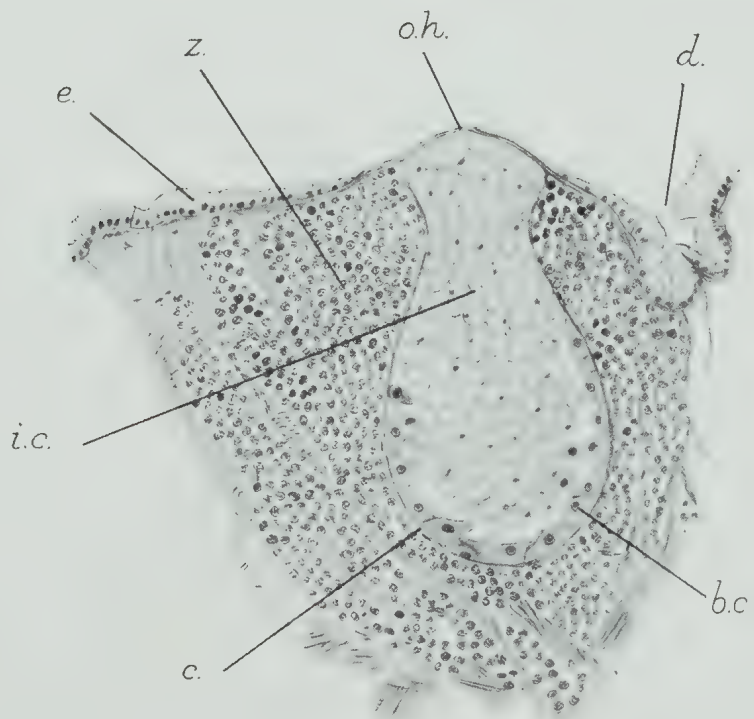
Brit. Mus. (Nat. Hist.).   REPORTS, VOL. I, No. 11.   PLATE V.

FIG. 11.

FIG. 12.

FIG. 13.

FIG. 14.

C. M. Yonge del.]   Adlard & Son. Ltd., Impr.